Juvenile primates in the context of their social group: a case study of chacma baboons (Papio ursinus) in an afro-montane environment

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Abstract

The prolonged juvenile period between infancy and reproductive maturity is the life history trait that best separates primates from other mammals. Juvenile primates are also the most neglected subjects of primatological research. The principal aim of my study was to examine the behaviour of juveniles and how they compare to older individuals, and in doing so, site this behaviour within the context of a social group of chacma baboons (*Papio ursinus*).

I collected data on a group of baboons in the Soutpansberg Mountains of South Africa over a 19-month period. I took a multi-faceted approach, using data collected though scan samples, focal animal samples, and GPS data to examine age and sex differences in behaviour. I analysed these data using several methods, including methods novel to primatological studies.

My results indicate that activity budgets and use of vertical space differ by age and sex. As a consequence of this variation in the time spent engaged in activities, I found that chacma groups exhibit low levels of behavioural synchrony as measured by the Kappa coefficient of agreement. My results also indicate that, despite being part of cohesive group, individuals also differ in their movements through the landscape. Individuals that received more agonism from other group members were found to be more constrained in their movements, travelling shorter, but more tortuous routes. My findings also show that young juveniles position themselves spatially in order to have more neighbours in proximity than older individuals, while social interactions amongst group members exhibit phenotypic assortativity, particularly amongst individuals of similar ages.

The behavioural differences found in juveniles relative to older conspecifics arise as a consequence of juveniles' priorities in not only surviving to adulthood, but also in ensuring future success as adults, with obligate group-living an important factor in the emergence of such differences.

Juvenile primates in the context of their social group: a case study of chacma baboons (*Papio ursinus*) in an afro-montane environment

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associated ($p<0.05$ * $p<0.01$**, $p<0.001$***). AM = Adult Male; AF = Adult Female; AdM = Adolescent Male; AdF = Adolescent Female; Pb = Pubescent (male only); OJM = Old Juvenile Male; YJM = Young Juvenile Male; YJF = Young Juvenile Female.

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Statement of Copyright

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1. Introduction

1.1. Primate Life History and the Juvenile Period

Primates are distinctive in that they possess a prolonged period of immaturity and slow growth rates compared to other similar sized mammals (Harvey & Clutton-Brock 1985, Charnov & Berrigan 1993, Kappeler et al 2003). This juvenile period, defined as the time between weaning and sexual maturity (Pereira and Altmann 1985, Setchell and Lee 2004), is arguably the single life history trait that best distinguishes Primates as an order, and yet it is the most neglected by researchers (Pereira and Fairbanks 2002, Pereira and Leigh 2003). While there are numerous reasons for this neglect, not least of which that juveniles are simply harder to study than adults, who are larger and more predictable, research on adults is the study of the relatively successful (Pereira and Leigh 2003). While there is a great deal of knowledge of the behaviour of adults of both sexes, there are significant gaps in our understanding of the path that immature primates take to get to adulthood (Pereira and Leigh 2003).

Immature primates experience far higher mortality rates than adults, with a study of 20 non-human primate species finding that on average 15% of juveniles die annually compared to only 8% of adults (Ross and Jones 1999). This increased risk is related to predation, with immatures being smaller and less competent at predator detection and evasion (and therefore easier prey), and malnutrition/starvation, as immatures are less skilled at finding and processing foods than adults and therefore at higher risk of energetic shortfalls (Janson and van Schaik 2002). An additional form of immature mortality, infanticide, comes from in the group itself and is characterised by the deliberate killing of infants by adult males (Hausfater & Hrdy 1984, van Schaik & Kappeller 1997), particularly in the case of newly immigrated males in species exhibiting male exogamy (Hrdy 1977).

The life history pattern found in primates has been viewed as being either adaptive in and of itself, or as a trade-off arising as a result of other adaptations (Ross 2003). Primates grow slowly relative both to other mammalian orders (Charnov 1993, Charnov and Berrigan 1993), and to what they are physiologically capable of (Janson & van Schaik 2002). This slow growth occurs even under food-enhanced conditions (Altmann & Alberts 1987). As a consequence, primates have later ages at first reproduction than similarly sized mammals (Charnov 1993, Leigh 2001). Moreover, they have small litters of only one or two offspring (Ross & Jones 1999). They also have relatively long gestation lengths, producing relatively large neonates (Charnov & Berrigan 1993, Kappeler et al 2003), which, combined with a long lacatational period and slow postnatal growth, require long interbirth intervals (Galdikas & Wood 1990). While this may be offset to some degree by the relatively long lifespans found in primates, even with this extended longevity female primates still have relatively few offspring during their life in comparison to other mammals (Charnov & Berrigan 1993). There has been much deliberation over this unique primate pattern, which can be summarised into three main hypotheses for the developmental evolution of the juvenile period and growth rates in primates (Ross & Jones 1999, Ross 2004) (Figure 1.1). While my intention in this thesis is not to test these hypotheses, I have presented them here as in order to place my study within a wider, developmental context.

1) Brain growth constraint model

Primates have relatively large brains, and the energetic requirements of this encephalisation may lead to primates saving energy in other organs, as the brain is energetically costly (Aiello & Wheeler 1995). As primate brains grow mainly before or soon after birth (Ross 2003), this leaves immatures with a particularly high relative metabolic cost, which may impose slowed somatic growth.

2) Needing to learn model

Large brains occur in species that need sophisticated information processing capabilities required for complex social and/or physical environments. As this depends on learning, these species will delay maturity until they have learned enough to be behaviourally mature, resulting in an extended juvenile period.

3) Juvenile risk model

As immature primates are smaller and less skilled than adults, they are at greater risk from malnutrition or predation (Janson and van Schaik 1993). While these problems mainly relate to their small body size, and could therefore be overcome by growing faster, primates instead grow more slowly. By reducing their metabolic needs through such slow growth, they increase long term survival.

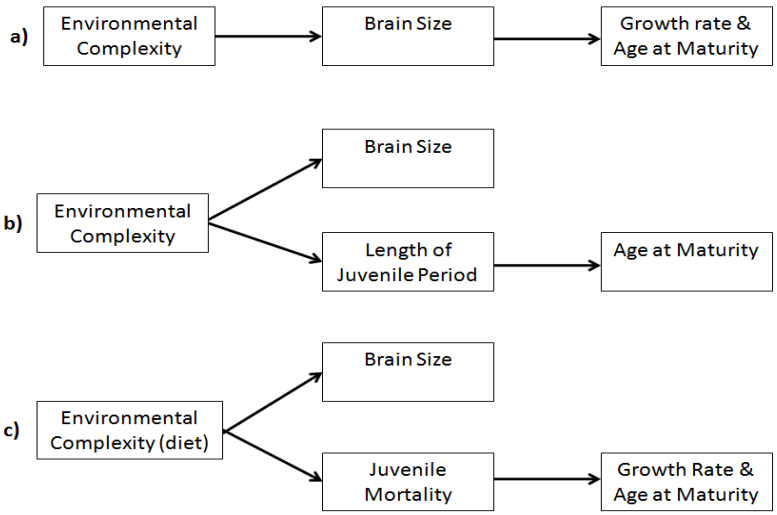

Figure 1.1: Suggested relationships between brain size, maturation age and environmental complexity in primates: a) Brain Growth Constraint model; b) Needing to Learn Model; c) Juvenile Risk Model. Adapted from Ross (2004) figure 8.4 p. 132

Phylogenetic analyses of life history variables for non-human primate species have provided conflicting evidence in support of these hypotheses. Some analyses suggest that the brain growth constraint model offers the best explanation for the distinctive brain and life history patterns found in primates (Ross and Jones 1999, Ross 2004, Barton & Cappelini 2011). Conversely, a strong negative relationship between Charnov's (1993) growth constant, *A* (a species-specific value employed in models of growth from weaning to adulthood via a 'growth law':$\frac{dW}{dt} - A\ x\ W0.75$, where *W* is body weight, *t* is age, and *dW/dt* is body growth rate at a specific time) and age at first reproduction and age at sexual maturity provides stronger support for the juvenile risk model than the

brain constraint model; slow growth in primates is related to high risk of predation and the high levels of feeding competition in large groups over patchily distributed resources (Mumby and Vinicus 2008). Furthermore, comparative studies have also provided evidence to support the suggestion that the juvenile period in non-human primates evolved as a response to social pressures and the requirements of learning and developing social skills, with the proportion of lifespan spent as a juvenile correlated with the relative size of the non-visual neocortex (associated with social problem-solving capabilities), and a correlation between social group size and the length of the juvenile period (Joffe 1997, Walker et al 2006). Importantly, hypotheses relating to correlations between life-history variables may be mutually compatible and cross-correlated themselves, particularly those relating to brain size and life-history in primates (Deaner et al 2003).

One of the key problems with analyses of primate life histories and socioecological component modelling is that different researchers, working on similar databases and using high levels of analytical rigour, can have very different findings, often dependent on the statistical techniques available (Ross 1998, Deaner et al 2003) or simply the quality of the dataset used (Borries et al 2013). For example, while earlier studies found a significant relationship between diet and brain size, with frugivorous primate species having relatively larger brains than similarly-sized folivores (Clutton-Brock and Harvey 1980; Foley and Lee 1992), later studies have not supported this relationship (e.g. Walker et al 2006). There is, however, one finding that is highly consistent across phylogenetic studies: the relationship between brain size and sociality. Initial reports that neocortex ratio and social group size/social complexity are highly related (Sawaguchi and Kudo 1990; Dunbar 1992) have been reliably reproduced in a number of studies (e.g. Barton 1996; Joffe 1997; Kudo and Dunbar 2001; Dunbar 2003; Dunbar and Schultz 2007), although there is increasing appreciation that it is not just the relative neocortex or brain size, but also overall brain size that is important in determining and predicting primate cognitive ability, of which social complexity is a key component (Deaner et al 2007).

The robustness of the relationship between brain size and social complexity has led to the development of a series of concepts once known collectively as the “Machiavellian

Intelligence Hypothesis" (Byrne and Whiten 1988, 1997), but now better known as the "Social Brain Hypothesis" (Barton and Dunbar 1997, Dunbar 1998). The expansion of brain size in primates is considered to be related to the requirements of living in complex social groups, and while ecological components certainly play a role, it is these social complexities that are considered to be the fundamental evolutionary pressures selecting for large brain size in primates (although see Clutton-Brock & Harvey 1980 for ecological pressures relating to spatial memory for patchy resources; Byrne et al 2001 for the cognitive requirements of extractive foraging; Povinelli and Cant 1995 for the requirements of arboreality in large-bodied primates as putative drivers of cognitive evolution in primates; and van Schaik & Bukart 2011 and van Schaik et al 2012 for the integration of social intelligence and cultural learning, the cultural intelligence hypothesis). Primate groups are generally composed of three or more mixed-sex adults and their dependent offspring (Kappeler & van Schaik 2002), and while there is both wide inter- and intra-specific variation in group sizes (Chapman 2012), communal living is a key feature of primate societies that sets them against other mammals. 73.2% of primate genera exhibit year-round associations between males and females, far exceeding the proportion of any other Order (range 12.5% in Perissodactyla to 31.8% in Carnivora, van Schaik & Kappeler 1997).

While the evolutionary pressures that have selected for enhanced brain size in primates are reasonably well understood (Dunbar & Shultz 2007), the pressures that have led to the extension of primate life histories, particularly the prolonged period of slow growth in the post-infant, pre-reproductive period, are as yet unclear (Borries et al 2013, Eadie 2015). This can be attributed to the lack of empirical studies focussing on juvenile primates, particularly those which examine juveniles alongside their mature conspecifics. Several recent studies have tried to address this situation, but have focussed mainly on foraging behaviours (e.g. squirrel monkeys *Saimiri sciureus,* Stone 2007; sooty mangabeys *Cercocebus atys,* McGraw et al 2011; ring-tailed lemurs *Lemur catta,* O'Mara 2015; tufted capuchins *Sapajus libidinosus,* Chalk et al 2015; capuchin monkeys *Cebus capuchinus* Eadie 2015). To better understand the evolution of the juvenile period in primates, it is important to understand how and why juveniles differ

in their behaviour relative to their older counterparts, particularly in the social context of group-living animals.

1.2. Juvenile Primate Behaviour and Development

Juvenile primates are generally regarded as being less successful at foraging than older individuals (Altman 1980, Janson & van Schaik 2002). While they average around 50-70% of adult female body weight, and should therefore be expected to require 60-80% of an adult females energy intake, based on allometric scaling, they actually spend more time feeding than adult females (median 105% of adult female time, Janson & van Schaik 2002). Juvenile primates may require more time to process foods than adults (Post et al 1980), and may also be restricted in their abilities to process and consume certain food items leading to differences in the time spent feeding on different items (Harrison 1983). Where food items are difficult to process, juvenile primates may acquire knowledge through the observation of adult group members, although there is wide variation in such social tactics of food acquisition during ontogeny in Primates (Rapaport & Brown 2008).

The evidence in support of juveniles' feeding efficiency or processing abilities being lesser than adults is inconclusive, and varies across species and dietary items. For example, adult capuchins (*Cebus capuchinus*) had higher foraging return rates than immature individuals for difficult to acquire food items, but not for easier items (Eadie 2015). Likewise, young juvenile geladas (*Theropithecus gelada*) prefer less tough food items than older individuals (Venkaraman et al 2014), while juvenile long-tailed macaques (*Macaca fasicularis*) avoid difficult food items (van Schaik & van Noordwijk 1986). Conversely, studies of sooty mangabeys (*Cercocebus atys,* McGraw et al 2011) and tufted capuchins (*Sapajus libidinosus,* Chalk et al 2015) found juveniles to be almost as capable as adults in processing difficult food items, while ring-tailed lemurs reach adult levels of foraging efficiency by the age of one year (O'Mara 2015). Juvenile primates may be restricted in the food items they can process not only from a lack of experience, but also from a lack of physical strength, particularly in the case of extracting

hard to access food sources such as hard-shelled fruits, embedded vertebrates, and subterranean grass corms (Fragaszy & Boinski 1995, Altmann 1998, MacKinnon 2005).

It is likely that the majority of primates' learning about food items may have already taken place during their infancy (Joffe 1997), and indeed the diet of primates near the point of weaning has been found to act as a predictor for adult fitness (Altmann 1998). Improvements in foraging efficiency tend to level off before the end of the juvenile period (Janson & van Schaik 2002), and older juveniles tend to be more similar to adults than do young juveniles (O'Brien & Kinnaird 1997). However, even if juveniles are not limited in their foraging or food processing abilities, their small body sizes may allow them to access foods inaccessible to larger, heavier adults (Menard 1985, Menard & Vallet 1986).

While the acquisition of food resources is vital for survival, immature primates must also develop their social skills, and one of the hallmarks of young primates is their capacity for play (Poirier & Smith 1974, Lewis 2000). Play generally decreases through ontogeny, occurring most in infants and young juveniles, and decreasing in the later juvenile period until virtually absent in adolescence and adulthood (Fagen 2002). In addition to having a valuable role in the development and maintenance of social relationships (Poirier & Smith 1974), play has been linked to the development of the central nervous system, with rates of play in vervet monkeys (*Chlorocebys pygerythrus*) peaking at the same time as synaptic densities in the motor and visual cortices in the neocortex (Fairbanks 2000). Social play has a further role by stimulating the neuromotor connections, enabling further complexity of coordination (Pereira and Leigh 2003). Juvenile play partners are often chosen based on body size and sex (Pereira and Altmann 1985, Owens 1975a). Immature primates also need to develop a sophisticated knowledge of their conspecifics to ensure both survival to adulthood, and subsequent success (Pereira 1988).

Primates show partner preferences on the basis of kinship, dominance and affiliation (or friendship) (Tomasello & Call 1997). Of these, the most salient is preference based on shared kinship, for example between maternally-related adult females in female-bonded cercopithicine species (Gouzoules & Gouzoules 1987), although there is also evidence that shared paternity may also play a role in kin-biased behaviour (Widdig et

al 2001, Smith et al 2003, Kazem & Widdig 2013). Biases related to dominance often take the role of avoidance or submissive behaviours, but dominant individuals may also be more attractive as social partners to lower-ranked individuals, who prefer to associate with those ranked higher than themselves (Cheney 1977; O'Brien & Robinson 2002). Finally, biases related to preceding agonistic and affiliative interactions have been found in several species, such as postconflict 'reconciliation' (de Waal 1989) or assisting in others' conflicts following grooming (Seyfarth & Cheney 1984). Most primates also exhibit a marked degree of diethism on the basis of sex, with these differences emerging in the juvenile period (Pereira & Altmann 1985). The inherent complexity of primate social environments requires immatures to develop their knowledge of other individuals in their group as they mature.

Social ontogeny refers to the social development of an individual (Deputte 2000), with social behaviour developing interactively via social encounters with other group members and involving two inter-dependent processes: the acquisition of a social behavioural repertoire, and the development of a social network (Deputte & Quiris 1996). While the first of these processes is connected to the more general process of behavioural and social development, the second requires a constant reshaping of the behavioural repertoire (Deputte 2000), and therefore considerable flexibility. An individual's behaviour depends on the preceding interactions with other group members (Altmann 1965), guided by trial-and-error learning or ontogenic ritualization (Tomasello and Call 1997), a process through which repeated iterations of social interactions with other group members helps the acquisition of social skills. As a young primate matures, the relationships that it has with conspecifics are likely to change, particularly as they will constitute a greater competitive threat to other group members. For example, while a young individual may be able to forage in close proximity to other group members and still meet their calorific requirements (Janson & van Schaik 2002), and even preferentially associate with adults more likely to allow them access to food (Pereira et al 1988), as it matures it is less likely to be tolerated by other group members (Horrocks and Hunte 2002).

The ecological and social priorities of juvenile primates are therefore likely to be different relative older group members, with a resultant impact on the time allocated to

different activities (Singh & Vinanthe 1990, O'Brien and Kinnaird 1997, van Noordwijk et al 2002). In a group of animals in which individuals spent different amounts of time engaging in activities, they will alsoengage in different activities at different times, which may lead to a low level of behavioural synchrony (Ruckstuhl 1998, Conradt & Roper 2000). To date, only one study has explicitly addressed the issue of behavioural synchrony in primate groups, focussing on the influence of reproductive status on the activity of adult females (King and Cowlishaw 2009). A better understanding of age-related variation in activity budgets, and the associated effect this has on the extent of behavioural synchrony in primate groups is a promising avenue of research.

Most primates live in groups, and, with the exception of fission-fusion societies, travel together as a group (Bates & Byrne 2009). Being part of a group has many advantages, including decreased risk of predation (Janson 1990), increased potential for social learning of diverse skills (Lefebre 1995, Whiten 2000), and the communal defense of resources (Wrangham 1980). However, group-living also leads to the potential for intra-group competition, and larger groups require individuals to travel further to obtain resources as a consequence of food patch depletion and avoidance of other foraging animals (Chapman & Chapman 2000, Gilespie & Chapman 2001). The prolonged juvenile period may act to mitigate the impact of within-group competition on young primates, by not only reducing the likelihood and risk of such competition, but also allowing them the time to develop social strategies and the experience to improve their success as adults themselves (Perera 1988). However, while there is some evidence that individual movement patterns in a group vary with dominance rank (e.g. Isbell 1999b, Beisner & Isbell 2009), the effects of group-living on the movement patterns of juvenile primates are virtually unknown. Examining the effect of within-group competition on how individuals travel through the landscape, and whether juveniles are affected differently than older individuals will address this gap in our knowledge of group-living primates.

In addition to within-group competition, it is also important to examine the general patterning of relationships among individuals of different ages and sexes in a group, both affiliative and agonistic. Several studies have found that relationships between immature group members exhibit similar patterns to those of their same-sex adult conspecifics (Noordwijk et al 2002, Strier et al 2002, Cords et al 2010, Barale 2015).

Others have shown that primate groups exhibit assortative mixing whereby individuals exhibiting similar characteristics such as rank, age, sex, personality or reproductive status form bonds with one another due to commonalities in needs and experience (de Waal & Luttrell 1986, Matsumura & Okamoto 1997, Massen & Koski 2014, Carter et al 2015). No study on primates has as yet assessed the extent to which the patterning of different types of interactions exhibits such assortative mixing among individuals in a group (although see Carter et al 2015 for grooming and proximity networks). Through examining the relationships between and among individuals of different ages and sexes, and determining whether or not these observed patterns differ from what might be expected on the basis of group composition, we can develop greater insights into the social environment that juveniles face, and how this compares to that of older conspecifics.

1.3 Baboons as a study species

Baboons (*Papio* spp.) are among the most widely distributed primates in Africa, and are characterised by a high degree of behavioural and ecological flexibility (Henzi & Barrett 2005). They are probably the most intelligent of the Old World monkeys (Parker 2004). There are five 'classical' baboon types (chacma baboon (*Papio ursinus*), olive baboon (*P. anubis*), yellow baboon (*P. cynocephalus*), Guinea baboon (*P. papio*) and hamadryas baboon (*P. hamadryas*), Hall 1970), but there is debate as to whether these represent separate species (Groves 2001), or should be classified as subspecies in the *P. hamadryas* superspecies (Jolly 2003). Recent phylogenetic studies (Zinner et al 2011, Zinner 2013) recognise these five traditional types as separate species, while also contending that an additional species, the Kinda baboon (*P. kindae,* Rogers et al 2004) should be recognised. At points of contact through their ranges, these species readily hybridise (Barrett 2009). With the exception of hamadryas baboons, whose social organisation is comprised of one male and several females, and where both sexes may emigrate from the natal group (Kummer 1968, 1995), and possibly Guinea baboons (Jolly 2009, Kopp et al 2014), baboons live in multi-male multi-female matrilocal groups, with males tending to disperse to other groups (Altmann & Alberts 2003).

Baboons are highly sexually dimorphic with males being approximately twice the mass of females and having longer canines (Popp 1983). Female rank is inherited through matrilines, with the youngest female daughter attaining the rank below her mother (Cheney & Seyfarth 2007). The female dominance hierarchy is firmly enforced and transgressions punished (Owens 1975b). In contrast to the stability inherent to female dominance and rank, male dominance is ephemeral and unstable, with males changing dominance status many times over their lifetimes (Strum 2001). Among the baboon types, chacma baboon (*P. ursinus*) populations are characterised by a relatively short duration of alpha male tenure (between 7 to 8 months in the Okovango Delta, Botswana, Cheney & Seyfarth 2007). This is related to a high level of infanticide, in which a new male enters the group and kills existing infants to facilitate the resumption of reproductive cycling in resident females (Palombit et al 2000). For example, in a 10 year study of chacma baboons at Moremi Game Reserve, Botswana, 38% (46 out of 120 with a mortality rate of 0.21) of infants born died before reaching 1 year of age, with 25 of these deaths being either confirmed or suspected infanticide (Cheney et al 2004). For juveniles and adult females in contrast, the main cause of death was predation, with adult female mortality rate (0.09) higher than that of juveniles (0.04) (ibid.).

As a counter-strategy to infanticide, among the strongest associations, or friendships, found among chacma baboons is that between a lactating female and an adult male, who is likely to be the father of her offspring based on consortships during the reproductive period (Moscovice et al 2010). This preferential relationship between the 'protector' male and an associated infant carries over into the juvenile period, although adult males also assist the juvenile offspring of their former friends even when paternity is uncertain (Moscovice et al 2009). Chacma baboon infants and juveniles therefore have both maternal and (putative) paternal influences on their development.

Male baboons take approximately twice as long as females to reach full sexual maturity and adult body size (10 years versus 5 years) (Altmann et al 1977). Several studies have examined growth rates in baboons, finding that, for example, while male and female growth rates are quite similar up to 5.5 years of age (0-2 years – 6.7g/day female; 5.6g/day male: 2-5.5 years – 5.8g/day female; 5.9g/day male), growth rates then greatly diverge, with males growth accelerating to 9.8g/day and females declining to 5.4g/day

(Johnson 2003). Both growth rates and adult body size are greatly affected by food availability (Altmann and Alberts 2005). However, despite this very prolonged period of growth, in contrast to other papionins there is very little brain growth in the post-birth period; baboons are born with brain sizes very close to those of adults (Pereira and Leigh 2003). This is thought to be an adaptation to the pressures that immature baboons face, with the energetic requirements for growing a large brain placed on the mother, rather than the infant (Leigh et al 2003). While there is evidence that foraging skill is a key cognitive driver in baboons, with foraging success in the first 30-70 weeks of life predicting lifetime fitness (Altmann 1998), it is also possible that this unique baboon pattern is related to social complexity.

Much of what we know about the behaviour of immature baboons comes from studies examining either play (Owens 1975, Cheney 1978, Chalmers 1980, Coehlo & Bramblett 1982) or rank acquisition (e.g. Cheney 1977, Lee & Oliver 1979, Johnson 1987, Pereira 1988b, 1989), with sex differences being a key feature. Male juveniles play more often and more roughly than females (Owens 1975), and while juvenile females are restricted in their abilities to attain high ranks as a consequence of their own mothers' rank, juvenile males are effectively able to attain as high a rank as they are capable of through their own efforts (Pereira 1989). Play behaviour and the acquisition of rank are likely to be related, but juvenile baboons do not exist in a vacuum, and are reliant upon the support and tolerances of their adult conspecifics. It is therefore vital to examine the behaviour of juvenile baboons in the context of group-living, and relative to the behaviours of their older conspecifics.

1.4. Thesis Aim

The central aim of my thesis is to examine age and sex related differences in primate behaviour, specifically relating to aspects of living within a social group. Studies on primates have often been focussed on only one-particular age class, most notably adults of either or both sexes. Through examining immature and mature members of the same social group, I aim to add to our knowledge of how group-living may have variable

effects on such individuals' dependent upon their own priorities and position, both spatially and socially, within a group..

To meet this aim, I take a multi-faceted approach to examining behavioural differences in a group of baboons. I examine the general activity budgets of animals in different age and sex classes, whether different aged animals engage in the same activity at the same time and the extent to which they exhibit behavioural synchrony. I also examine the impact of within-group competition on individual movement patterns, characterised as the extent of agonism received by individuals of different ages and sexes as they move through the landscape. Finally, I examine age and sex related variation in social spacing and the patterning of social relationships among individuals in the group.

1.5. Thesis Outline

In the next chapter I introduce the study site and subjects, along with the data collection methods I used. In Chapter 3 I describe age and sex related differences in the allocation of time to general activities, the time spent at different heights above the ground and the time spent engaging in different activities on or above the ground. Chapter 4 examines the extent to which individuals in the group are engaged in the same activities at the same time (i.e. their behavioural synchrony). In this chapter, I also examine the impact of group composition on behavioural synchrony, by dividing the data into mature-only and immature-only groups, and examine the effects of different levels of behavioural categorisation on behavioural synchrony. In Chapter 5 I use a combination of behavioural observations and GPS data collected via focal animal sampling to test the effects of age, sex and social dominance on the distance travelled and the tortuosity of movement by individuals. In Chapter 6 I investigate the effects of age and sex on social spacing, along with the extent to which individuals associate with one another according to phenotypic homophily or heterophily. Finally, in Chapter 7 I discuss the findings of my research and present the conclusions of my study.

2. Methods

2.1 Study Site

I collected data over 19 months (November 2011 to June 2013) at Lajuma Research Centre (Lajuma) in the Soutpansberg Mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S, Figure 2.1). Due to the high biodiversity in the Soutpansberg mountains, several landowners and stakeholders in the Western Soutpansberg applied for and were granted Natural Heritage Site status in 1997, and in 2009 the Soutpansberg Mountains were incorporated into the wider UNESCO Vhembe Biosphere Reserve (30,701km^2, http://www.vhembebiosphere.org/about-vbr).

Figure 2.1: Location of the Soutpansberg Mountain range (red) and the location of Lajuma Research Centre near the Western boundary (white arrow) (from Willems 2007)

2.1.1 Geology and Topography

The Soutpansberg range was formed around 1,800 million years ago as an east-west trending assymetrical rift (Brandl 2003). The range extends approximately 210 km, from Vivo in the west to Punda Maria in Kruger National Park to the east (23°05'S & 29°17'E

to 22°25'S & 31°20'E), with a maximum width of 60 km, encompassing a total area of 6,800 km^2 (McDonald et al 2003). The composition of the rock formations is primarily sandstone, quartz sandstone and quartite, with some igneous intrusions of basalt and dolerite. Successive faulting in an ESE to WSW direction has caused the strata to dip in the north and rise in the south. As a consequence the Soutpansberg are the most intensively block-faulted sequence in South Africa (McDonald et al 2003), leading to a characteristic system of horizontal 'layers' with steep vertical faces. Along the Soutpansberg range, altitude varies from 200m to 1747 m, and the elevation at Lajuma range from 1150m to a peak of 1747 m, including the highest peak of the Soutpansberg range (Mount Letjume).

2.1.2 Climate

The climate of the Soutpansberg range is best classified as temporate/mesothermal (Willems 2007) with two main seasons: the warm wet season (December to February) with temperatures ranging 16-40 ^{0}C, and the cool dry season (May to August), with temperatures ranging 12-22 ^{0}C (Kabanda 2003). The east-west orientation of the mountain range forms a barrier between the maritime climate in the south-east and the continental climate to the north, and also affects wind patterns (de Raad 2011). This means that the climate is highly variable throughout the range, particularly with regards to rainfall which can range from 340 mm per year in the far western regions to 2,000 mm per year in the centre of the range (Kabanda 2003). Additionally, the orographic mist along the southern slope may increase known precipitation values far in excess of standard rainfall estimates, with one area (Entabeni) receiving 1,874 mm of rainfall but a total precipitation of 3,233 mm once mist is accounted for (Mostert et al, 2008). This mist-belt zone accounts for greater than 40% of the total annual precipitation (South African Department of Environmental Affairs, 1988), such that measured rainfall at Lajuma underrepresents the actual levels of precipitation (Willems 2007).

Local climatic data at Lajuma were collected by a weather station positioned at 1270 m with this data being available from 22 July 2010 through to 14 June 2013 (Figure 2.2). Data were recorded at 30 minute intervals throughout this period. Due to technical

problems downloading the data from the weather station, data are missing for 15/09/2011 - 05/10/2011 and 12/12/2012 - 13/12/2012.

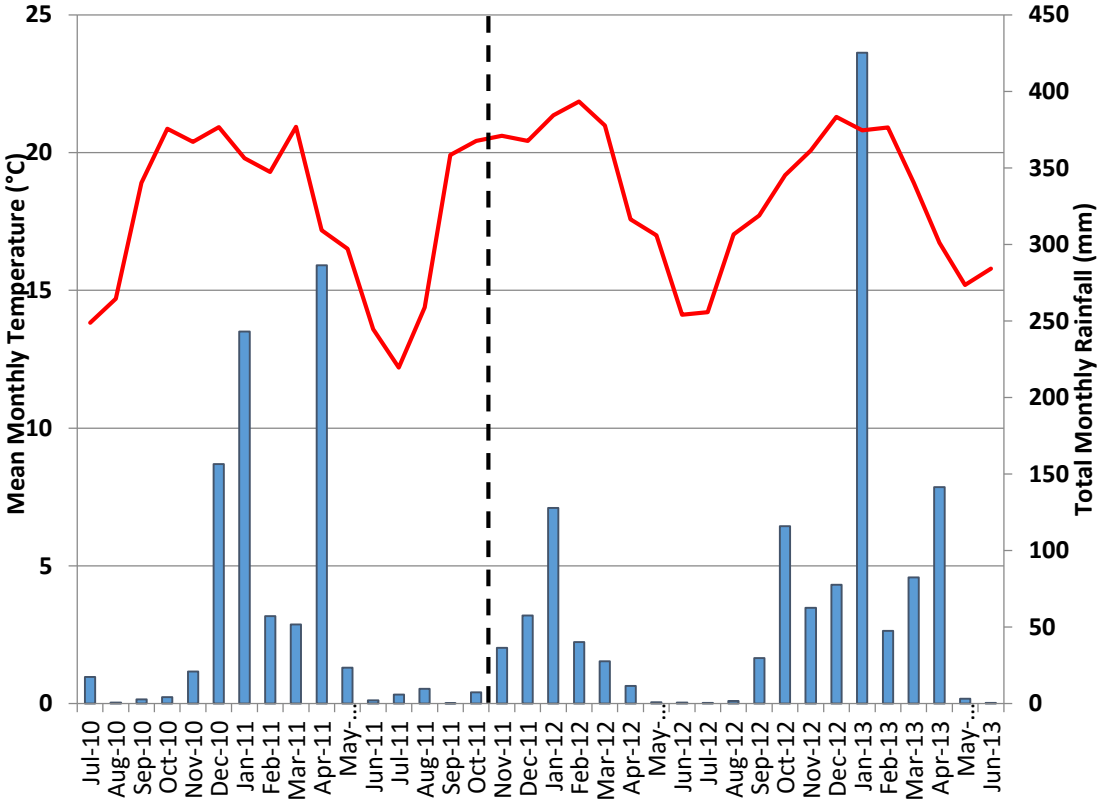

Figure 2.2: Mean monthly temperature (red line) and total monthly rainfall (blue columns) for July 2010 to June 2013. The dashed line indicates the beginning of data collection

2.1.3 Flora and Fauna

The study area comprises a mosaic of differing habitat types due to topographical and microclimatical features, and has been recognised as having rich diversities of plant communities relative to size of the area (van Rooyen & Bredenkamp 1996, van Wyk and Smith 2001). While an earlier study detailed three main vegetation types (Northern Mistbelt Forest, Soutpansberg Mountain Bushveld and Soutpansberg Summit Bushveld, Musina and Rutherford 2006), a more recent synthesis revealed eight major vegetation types in the Soutpansberg and neighbouring Blouberg regions (Mostert et al 2008). Five of these habitat types are present at the study area (de Raad 2012, Linden et al 2014):

a) Soutpansberg Arid Northern Bushveld (*Adansonia digitate – Acacia nigrescens*). Classed as open woodland, confined to the rain-shadow northern ridges of the region. Characterised by highly diverse plant communities adapted to water-stress conditions.
b) Soutpansberg Moist Mountain Thickets (*Catha edulis – Flueggia virosa)*. Classed as low, closed thickets with no defined separation between the tree and shrub layers and ranging from 1.5-4 m in height.
c) Soutpansberg Leached Sourveld (*Diplorhynchus condylocaropn – Burkea africana*). Relatively homogenous habitat of low species diversity of woody and grass species found in nutrient poor soils found in dry areas along the slopes of the mountain range.
d) Soutpansberg Cool Mistbelt (*Rhus rigida* var. *rigida – Rhus magalismontum* subsp. *codii*). Found at elevations >1200 m amongst the mistbelt zone. Contains extremely diverse plant communities characterised by a mixture of perennials not including any particularly dominant or abundant species, with distinctive bush clump communities found amongst open grasslands.
e) Soutpansberg Forest (*Xymalos monospora – Rhus chirendensis*). Confined to the southern slopes of the southern ridges of the mountain, comprised of tall evergreen forests surrounded by deciduous shrub forest thickets.

These different vegetation types lead to a high degree of biodiversity in the Soutpansberg, with plant species from 1066 genera and 240 families (Hahn 1997), along with 36% of reptile, 56% of bird and 60% of the mammal species found in South Africa present at the study site (Berger et al. 2003, Gaigher and Stuart 2003).

All five species of non-human primate found in South Africa are present at Lajuma: vervet monkeys (*Chlorocebus pygerythrus pygerythrus*), samango monkeys (*Cercopithecus albogularis schwarzi*), lesser bushbabies (*Galago moholi*), thick-tailed bushbabies (*Otolemur crassicaudatus*) and my study species, chacma baboons (*Papio ursinus*). Chacma baboons feed on both plant and animal food matter, and prey on termites, butterflies, young antelopes (bushbuck *Tragelaphus scriptus*, red duiker

Cephalophus natalensis and common duiker *Silvicapra grimmia*), crested guinea fowl (*Guttera pucherani*) and other birds and their eggs, lagomorphs (*Lepus* spp.), and vervet monkeys (Willems 2007).

Lajuma is also home to several predators of non-human primates, some of which are known to prey on baboons: leopards (*Panthera pardus*), crowned eagle (*Stephanoaetus coronatus*), Verreaux's eagle (*Aquila verreauxii*), and rock python (*Python sebae natalensis*). During my study, two baboons in my study group died as a direct result of failed predation events: a young juvenile male died from injuries sustained during an unsuccessful python attack, an infant male died from injuries indicative of an unsuccessful raptor attack. Three seemingly healthy females also disappeared at night. Based on the alarm calls heard at the field station from the direction of the sleeping cliffs on those nights they were probably predated by leopards.

2.1.4 Land Use Types

The study area is comprised of numerous small, privately owned properties of differing land-use types. At 4.3 km^2, Lajuma is one of the smallest properties in the area, and the study group ranged into all neighbouring properties. Two of these surrounding properties (Figure 2.3) presented significant challenges during fieldwork.

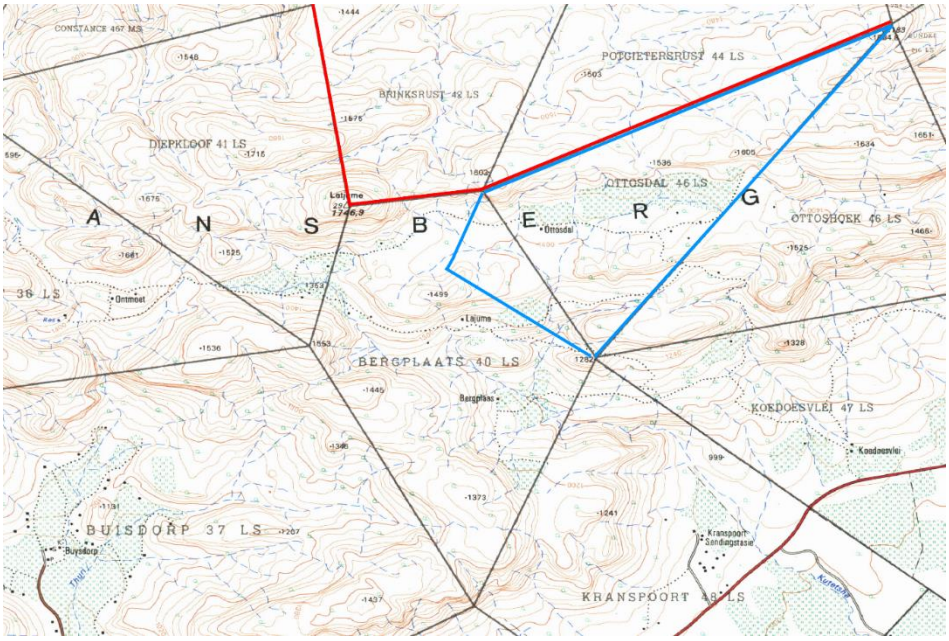

Figure 2.3: Boundaries of the properties encompassing the baboons range, with Lajuma at the centre (the northern section of Bergplaats). Sigurwana (red border) and Ottosdal (blue border) presented significant challenges for data collection

The first of these was a property to the North of Lajuma, Sigurwana. Sigurwana is primarily geared towards high-end tourism, and has introduced animal species not endemic to the area as a means of attracting customers. The property owners were cautious in allowing access to their property due to the economic value of these game animals and the potential risk of injury to animals who were not habituated to people walking on foot. I arranged a meeting with the property owners, and we were able to reach an agreement to allow restricted access to the property, provided that I could contact the manager of the property in advance. Unfortunately, the only way to contact the manager was by mobile phone, and there were very few areas where network signal was available. I was therefore seldom able to follow the baboons onto this property.

The second problematic property, Ottosdal, borders Lajuma to the East and Northeast. While historically this was a small-scale cattle farm, during my fieldwork the owners began clearing some areas of the property to cultivate avocado and macadamia nuts. This anthropogenic disturbance lead the baboons to change their ranging behaviour and avoid some areas. Once the land was cleared and the crops were planted, the owner did not want the baboons on his land. In May 2012 tensions reached a point at which the

landowner banned me from following the baboons on to his property. With the assistance of the owner of Lajuma, we managed to reach a compromise that would enable me to follow the baboons on this property but I was not allowed to enter the avocado plantation, or to come within 100 m of the farmhouse itself. As a result I was often only able to follow the baboons for a few hours from their morning sleeping site until they reached the areas I could not enter. I then waited until they emerged from these areas, but often lost the baboons as they moved up into the dense vegetation or up the side of the cliff to the rear of the property. I was only able to find them again on their return to the sleeping site in the afternoon.

2.1.5. Additional Information

The presence of multiple steep cliff faces between the different topographical levels at Lajuma meant that while the baboons had numerous safe sleeping sites, they were often difficult to follow. At many sleeping sites, the baboons either went up the cliff, or came down, and if I had positioned myself incorrectly I was unable to find them in the early morning. Baboons also often climbed up or down areas that were inaccessible to human observers during the day. I found alternate routes to follow them, but these invariably took longer than the baboons' more direct routes.

The dense vegetation made following the baboons difficult, but not impossible, in some areas. However, I suffered a back injury in March 2012 as a result of trying to follow the baboons through a dense acacia thicket. In October 2012 I was advised by my doctor and physiotherapist in South Africa to take 3 months rest to allow it to heal, so collected very few data between October 2012 and January 2013.

2.2 Study Population

I collected data on one group of baboons, the House Troop. House Troop was initially habituated in 2002-2004 by Tom Larimer at the request of the owner of Lajuma, and has since been studied intermittently (de Raad 2012, Howlett 2012, 2015). I had previous

experience with House Troop as a research assistant from February to November 2008, but when I arrived at the field site in February 2011 they had become unaccustomed to human observation. I began re-habituating the group in February 2011, and was able to collect data from November 2011. Even then, habituation was a continual process, with some individuals being wary of human observers for the duration of my study.

In the absence of long-term data on the dates of births and the identification of individuals, I estimated the ages of individuals using developmental and morphological indicators. On the basis of previous studies (Kummer 1968; Altmann & Altmann 1970, Altmann et al 1977, Sigg et al 1982; see also Whitehead et al 1990 for estimates of the ages of chacma baboon infants based on changes in ear and muzzle colour), the developmental stages reviewed in Setchell and Lee (2004), and personal observations in the field, I categorised animals as Infant, Juvenile, Pubescent, Adolescent and Adult, with sub-categories for infant, and juvenile (Table 2.1). While I could not census the group fully due to habitat conditions, I estimate that the group size was 72 individuals at the beginning of my study, and ranged ~70-80 individuals during the study.

From my previous experience with House Troop (as a field assistant) I was able to successfully re-identify several adult individuals. It took longer to learn the identities of younger individuals and some individuals were still not easily identified by the end of the study.

Table2.1: Age/sex class descriptions for chacma baboons and estimated population (N) at November 2011. Total population = 72, 35 males and 37 females.

Class	Physical Description	Age Estimate (years) [N]	
		Male	**Female**
Young Infant	Pelage initially black, transitioning to yellow/brown. Ears and muzzles turning from pink through to grey. Nutritionally dependent on lactating mother.	0-0.7 [3]	0-0.7 [2]
Old Infant	Pelage fully yellow/brown. Ears and muzzle completely grey. Nutritionally dependent on lactating mother, but undergoing weaning.	0.7-1.3 [2]	0.7-1.3 [3]
Young Juvenile	Fully weaned and nutritionally independent. Muzzle starts becoming more elongated and pronounced. Pelage still lighter than in adults.	1.3-3 [5]	1.3-3 [5]
Old Juvenile	Greater body size. Hair becomes darker, changing to a more adult grey/brown colouration.	3-5 [8]	3-4.5 [3]
Pubescent	***Males only.*** Body size that of an adult female, muzzle further extended to nearly that on an adult male. Testes start to expand and are clearly visible. Mane becomes noticeable.	5-7 [4]	N/A
Adolescent	***Males*** – Massive growth in secondary sexual characteristics; testes expand, canines and mane grow. longer, body size increases to near that of an adult male ***Females*** – Nearly adult female size, with the onset of the first sexual swellings.	7-10 [4]	4.5-6 [4]
Adult	***Males*** – All secondary sexual characteristics fully developed, musculature expands to full adult size. ***Females*** – Attainment of full body size, either cycling regularly, pregnant or lactating.	10+ [9]	6+ [20]

2.3 Data Collection

2.3.1 Scan Sampling

I collected scan samples (Altmann 1974) from dawn to dusk at 30 minute intervals for a maximum duration of 5 minutes. Beginning when the baboons emerged from the sleeping cliffs, and continuing until the majority of baboons descended/ascended the sleeping cliffs in the evening, I recorded the behaviour of all visible individuals along with socio-spatial and other general information (Table 2.2). Field assistants also collected scan data, once we reached 100% concordance on the identification of age and sex classes, the definitions of behaviours and heights above ground, and distances following several months of training. Due to the time required to identify individuals, we collected scan data at an age and sex level. As younger individuals were often difficult to sex, we collected data on infants and juveniles at age level only. To avoid sampling an individual more than once during a scan, we collected data either from front to back if the group was moving in any given direction, or from left to right if the group was mainly stationary. If we were unsure whether we had already recorded an individual in the scan, we did not record it again.

Scan data were collected for the purpose of identifying broad-scale differences in activity budgets and at age-sex class level (Chapter 3) and for the purpose of analysing the behaviours that animals were engaged in at the same time (Chapter 4). While activity budgets could be determined using the focal data collected (2.3.2), during the early phases of the study I recognised that the young juveniles would prove problematic for focal sampling due to difficulty encounted in following individual animals. The young juveniles were however amendable to data collection conducted by a more static observer, therefore the scan data represents the best method for examining age-related differences in activity budgets.

Table 2.2: Ethogram used in scan sampling

Category		Description
Environmental - Recorded once for each scan		
Date and Time		Date and time
Weather		(O)vercast – Mainly cloud cover (M)ist – Low lying cloud (R)ain – precipitation (S) – Mainly sunny
Habitat in which the majority of the group were found		Bushland – Predominately woody vegetation up to 1m in height Forest – Closed woody vegetation characterised by trees Grassland – Open landscape, mainly grasses Road – Anthropogenic travel routes used by vehicles Rocks – Rocky outcroppings Shrubland – Open landscape, mainly grasses by also some other vegetation up to 1m Swamp – Marshy areas along water courses Thicket – Closed woody vegetation characterised by thorny shrubs or trees
General Activity – Recorded for each individual in the scan		
Age and sex class		Young Infant Old Infant Young Juvenile Old Juvenile Pubescent Male Adolescent Male Adolescent Female Adult Male Adult Female
Feeding	Fruits/seeds	Consumption of fruits or seeds from trees or shrubs (e.g. waterberry fruits, acacia pods)
	Leaves	Consumption of leaves from trees or shrubs
	Grasses	Consumption of any surface grasses and their seeds
	Subterranean digging	Consumption/extraction of any plant based subterranean food items (e.g. grass corms, roots)
	Animal matter	Consumption of any animal matter (bushbuck, rock hare, termites)
	Drink	Imbibing of any water source
	Suckle	Consumption, or potential consumption of milk from mother's nipple
	Other	Consumption of any other food item
Travel	Locomote	Non-subsistence moving through trees or on the ground
	Carried ventrally	(Infants/juveniles only) Carried by mother or other group member ventrally
	Carried dorsally	(Infants/juveniles only) Carried by mother of other group member dorsally (jockey riding)
Social	Allogroom	Grooming/being groomed by another individual
	Autogroom	Grooming/inspecting self
	Play	Playing (either with self or with others)
	Sex	Any copulatory activity
	Aggression	Engaging in any aggressive behaviour (chasing, fighting)
	Other	Any other social behaviour
Resting		Inactive and immobile (sitting, lying, sleeping) :

	Covered Exposed	in a covered location in an exposed location
Travel Feeding		Movement involving picking up/searching for food items
Spatial – Recorded for each individual in the scan		
Estimated height above the ground	On the ground Between the ground and 2m above the ground 2-5m above the ground 5-10m above the ground 10m or more above the ground	
Number of neighbours	The number of other individuals within a 5m radius (counted individually until from 0-10, then approximated to >10, >15, >20 or unknown)	
Distance to nearest neighbour	Estimated distance to the closest individual (at 1 metre intervals for 0-10m, then approximated to >10 >15, >20 or unknown)	
Distance to mother	(Infants/juveniles only) Estimated distance to mother (at 1 metre intervals for 0-10m, then approximated >10 >15, >20 or unknown)	

We collected data using a spreadsheet programme (SpreadCE, Bye Design Limited http://www.byedesign.co.uk/) installed on PSION Walkabout Pro handheld computers. I chose this software as it allowed for the implementation of drop-down lists in each data cell (Figure 2.4), and I developed the spreadsheet to mimic traditional pen-and-paper data collection, allowing for the uploading of data without the need for transcription.

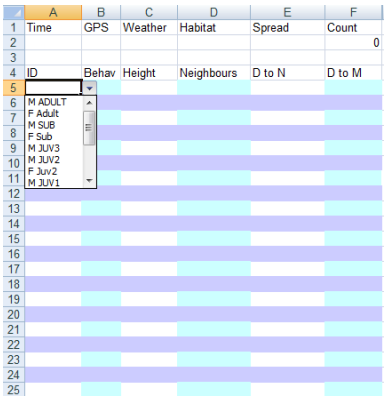

Figure 2.4: Example of the SpreadCE spreadsheet used for recording scan samples

We collected scan data over 19 months (November 2011-May 2013), giving a total of 1068 scans over 170 days of data collection, with 8.95 +- 5.83 days of data collection per month, and 6.32 +- 4.58 scans per day. In these 1068 scans, a total of 12,627 behavioural records were collected (Table 2.3), with the amount of data collected for each age-sex class broadly in line with their prevalence within the group's demography

(Figure 2.5). Due to the inaccessibility of the baboons, adverse weather conditions, recruitment and retention of assistants, and personal injuries, there was considerable variation between months in the amount of data collected (Figure 2.6). There was also considerable variation in the amount of data collected at different times of the day, with fewer data in the middle of the day (11:00-15:00) than in the early morning or late afternoon (Figure 2.7).

Table 2.3: Number of behavioural records collected in 1068 scan samples for each age and sex class

Age – Sex Class	Number of samples
Young Infant	67
Old Infant	314
Young Juvenile	948
Old Juvenile	1899
Pubescent Male	930
Adolescent Male	1189
Adolescent Female	1002
Adult Male	3197
Adult Female	3081
Total	**12627**

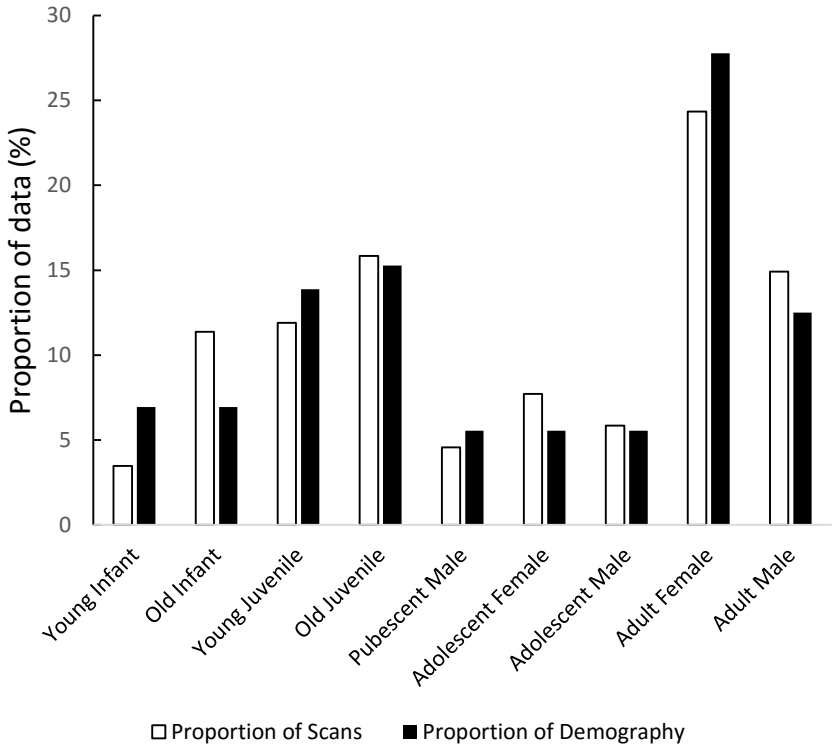

Figure 2.5: Proportion of total scan data collected along with prevalence in the group's demography by age and sex class

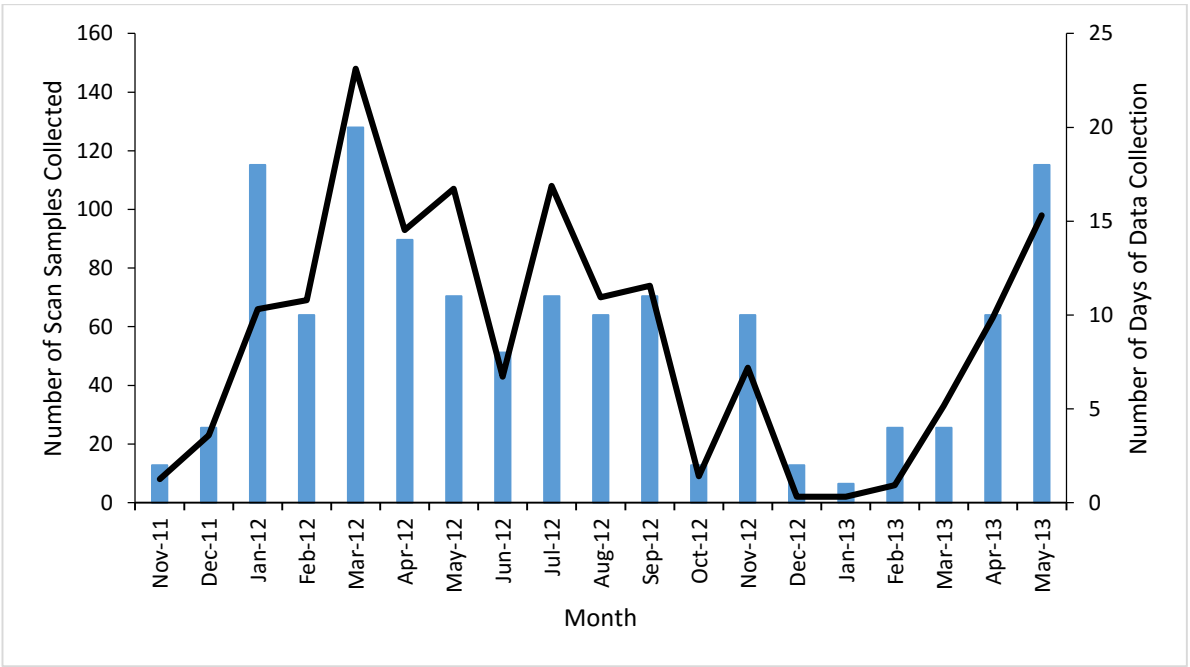

Figure 2.6: Scan data collected over the 19 month study. Blue columns indicate the number of days in which data were collected for each month, black lines indicate the total number of scans collected during each month

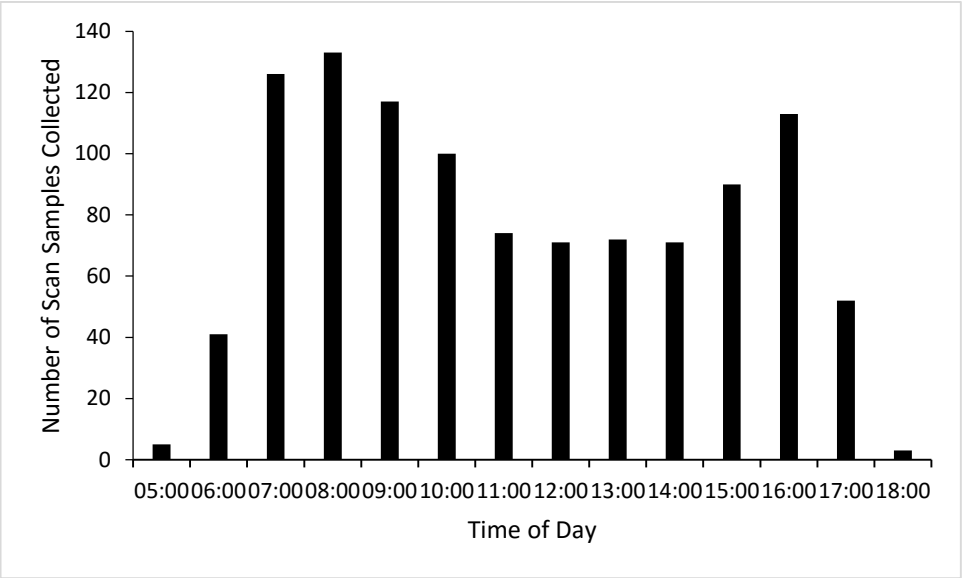

Figure 2.7: Total number of scan samples collected for each hour of the day throughout the study

2.3.2 Focal Animal Sampling

I conducted 15 minute continuous focal samples (Altmann 1974) using the Pocket Observer 3.1 (Noldus Software, www.noldus.com) software installed on a Psion Walkabout Pro PDA. I collected both continuous data (behavioural states) and instantaneous data (events) while maintaining constant visual contact with the focal subjects. In these focal samples I recorded the general activity, habitat type and level of exposure to the elements of the focal subject, along with their height above the ground, their number of neighbours and their distance to, and identity of, the closest neighbour. I also recorded every social interaction that the focal subject was involved in during the focal sample (both initiated by the subject, or directed by another individual towards the subject) along with the identity of the social partner, if known. I grouped social interactions into five main categories: spatial (any interactions involving a movement in to or out of proximity to another animal), vocal, agonistic (any aggressive or dominance-related interactions between individuals), affiliative (any prosocial interactions between individuals), and play (discriminated from aggression by the absence of threat behaviour, Owens 1975b, Cheney 1978) (Table 2.4).

Following Altmann (1965) I began with a limited interaction ethogram at the beginning of the study and added additional interaction types on an *ad hoc* basis as the full range of interactions and behaviours become apparent. I recorded all interactions on an elemental, dyadic basis. My final ethogram consisted of 53 behaviours (6 proximity, 12 vocal, 20 agonistic and 15 affiliative behaviours, Table 2.4). Given the complicated nature of these focal samples and the need to identify individuals accurately and quickly, I conducted all focal samples myself.

Focal data were collected for the purpose of examining individual differences in movement patterns (Chapter 6), and for the purpose of determining differences in social spacing and network assortativity (Chapter 7). As scan data were collected at an age-class level, rather than at an individual level, the greater precision implicit with focal sampling allows for higher level analyses of behavioural differences at an individual level, while also allowing for the collection of multiple forms of continuous data simultaneously.

Table 2.4: Ethogram for data collection during focal animal sampling

Continuous Variables **Environmental**		
Habitat		See Table 2.2
General level of exposure and cover:		Covered – In thick vegetation or terrain, fully shaded Semi-exposed – In intermediate vegetation or terrain, shaded Exposed – In a completely open environment, no shade
Activity		
Feeding		See Table 2.2
Travel	Locomote	Non-subsistence moving through trees or on ground
Social (durational interactions)	Allogroom	Grooming/being groomed by another individual
	Autogroom	Grooming/inspecting self
	Play (from Owens 1975a)	Playing (either with self or with others) Wresting - Both interacting parties active, rolling around, biting etc Mauling - One partner inactive during play – one-sided Sparring - Partners facing one another, grappling and hitting towards head Mock biting - Soft biting or mouthing of social partner Chase – Chasing another individual
	Sex	Any copulatory activity
	Other	Any other social behaviour
Resting		Inactive (sitting, lying etc)
Travel Feeding		Movement involving picking up/searching for food items

Out-of-Sight	Focal animal not in view	
Spatial		
Estimated height above the ground:	On the ground Between the ground and 2 m above the ground 2-5 m above the ground 5-10 m above the ground ≥10 m above the ground	
Number of neighbours	The number of other individuals within a 5m radius (counted individually from 0-9, then approximated to >=10 or unknown)	
Distance to nearest neighbour	Estimated distance to the closest other neighbour, with the neighbours identity recorded Touching Between touching distance and 2m 2-5 m 5-10m >10m Unknown	
Behavioural Events – All recorded as either the focal animal receiving or given the interaction, along with the identity of the social partner if known.		
Spatial	Approaches	Animal moves to within touching distance, within 2 m, or to within 5 m of another animal
	Departures	Animal moves out of proximity to another animal, recorded to the same distances as approaches
Vocal	Chatter	Rapid, high pitched grunts
	Copulation call	Copulation call during sex (females only)
	Cry	Distress call intermediate between loud call and scream
	Keck	Short, sharp vocalization
	Loud call	Loud, piercing contact call
	Move grunt	Soft grunts in a non-social context
	Passive grunt	Rapid soft grunts
	Scream	Loud, high pitched vocalisation
	Threat grunt	Loud, sharp grunt to another individual
	Wahoo	Male version of the loud call
	Weaning	'Begging' vocalisations made by infants trying to access mothers nipple
	Other	Any other vocalisation
Agonistic	Attack	Sustained assault on another individual
	Bite	Physical attack on another individual with mouth/teeth
	Chase	Chase another individual
	Displace	Move an individual from their position
	Eyebrow flash	Raise eyelids at another individual
	Fear grimace	Teeth bared in an agonistic context
	Fight	Both individuals assaulting each other
	Flee	Runaway from another individual with tail erect
	Grab	Aggressively embrace another individual
	Hit	Physical attack with hands
	Hold down	Physically restrain another individual on the ground
	Ignore	Ignore the agonistic behaviours of another individual
	Lunge	An aggressive movement towards another individual
	Present	Presenting hind-quarters in an agonistic context
	Rub	Rub hand (usually right) on the ground/other substrate
	Supplant	Move and replace an individual from their position

	Teeth Chatter	Rapid gnashing of the teeth, may make a sound
	Threaten	Open mouth (no teeth showing) staring at another individual with ears flattened
	Vocal chase	Chase another individual while making wahoo vocalisations
	Yawn	Open mouth, bared teeth display
Affiliative	Anogenital inspection	Inspect/investigate hindquarters of other individual with muzzle or hands
	Come-hither-face	Facial expression signifying desire for social contact
	Copulation	Sex
	Embrace	Short duration physical contact
	Huddle	Long duration physical contact
	Ignore	Ignore the affiliative behaviours of another individual
	Infant hold	Hold an infant
	Infant inspection	Inspect an infant
	Lipsmack	Rapid movement of lips; may make a sound
	Mount (sexual)	Mounting another's hindquarters (sexual)
	Mount (social)	Mounting another individual in a non-sexual context
	Muzzle inspection	Sniff the muzzle of another individual
	Penis grab	Touch/stroke penis of another individual
	Present (grooming)	Present body part for grooming
	Present (sexual)	Present hindquarters for copulation

I could not collect focal samples on individuals following a predetermined schedule due to the difficulty of finding specific individuals, as the group was often widely spread and in dense vegetation or otherwise topographically challenging areas. Instead, I collected data in an opportunistic manner using the following rules to maintain independence of samples: i) no individual was sampled on more than one occasion on any day; ii) no individual was sampled in the same time-block (before 09:00, 09:00-12:00, 12:00-15:00, after 15:00) on consecutive days; iii) following a focal on an individual from one age-sex class, the subsequent focal was conducted on an individual from a different class; iv) focal subjects could not be within 5 m of the previous focal subject. While I was usually able to adhere to these sampling rules, in instances where the group was very spread out, or split into smaller subgroups, I broke these rules to continue collecting data.

I terminated a focal sample if the focal animal was out-of-sight for more than 2 minutes within the first 10 minutes. If the animal went out-of-sight after 10 minutes of data collection, I kept the data and continued searching for the animal until the 15 minute period was over. While most individuals were relatively easy to sample for the full 15 minutes, some individuals, particularly young juveniles were rarely successfully sampled as they disappeared into dense vegetation or simply ran away. To avoid undue stress to

the animals, I also terminated focal observations when the focal subject was clearly distressed by being followed (i.e. directing threats or fear calls towards me, conspicuously watching me, or moving in a manner that deliberately placed obstacles between themselves and me). I estimate that for every two successful focals, one was terminated early for these reasons.

I collected focal data over 18 months (Jan 2012 - June 2013). A total of 1,682 focals (420.50 hours) were collected over 189 days, with 10.5 +- 5.9 follow days per month and 8.9 +- 6.33 focal samples per follow day. I conducted focal samples on 54 individuals (mean number of focal samples per individual = 31.14, SD = 26.05, range 1-87, Table 2.5). As with the scan data, the amount of data collected varied considerably between months (Figure 2.8) and by time of day (Figure 2.9).

Table 2.5: Details of focal animals and number of focal samples collected

ID	Sex	Age at January 2012	Age at June 2013	Number of Focals	Notes
at	Female	Young Juvenile	-	**3**	
bd	Female	Young Juvenile	-	**43**	
bo	Female	Adolescent	Adult	**76**	Became adult October 2012. Gave birth 04/04/2013
bh	Female	Adult	-	**3**	
ca	Female	Young Juvenile	-	**1**	
el	Female	Adult	N/A	**2**	Died November 2012
ff	Female	Old Juvenile	Adolescent	**78**	Became Adolescent July 2012
fr	Female	Adult	N/A	**7**	Died September 2012
gr	Female	Old Juvenile	Adolescent	**53**	Became adolescent May 2012
hm	Female	Adult	-	**20**	Gave birth 14/06/2013
lo	Female	Adult	-	**21**	Fitted with a GPS collar on 09/03/2013
ma	Female	Adult	-	**33**	Gave birth 20/07/2012. Infant died 07/02/2013 as a result of injuries sustained from a failed eagle predation event. Fitted with a proximity collar 28/02/2013
me	Female	Adult	-	**20**	Gave birth 04/06/2013
ni	Female	Adult	N/A	**2**	Died January 2012
pe	Female	Adult	-	**14**	
pi	Female	Old Juvenile	Adolescent	**70**	
ry	Female	Adult	-	**1**	
sc	Female	Adolescent	Adult	**45**	Gave birth 17/10/2012
sh	Female	Adult	-	**4**	Gave birth 20/10/2012
sf	Female	Adult	-	**43**	Gave birth 26/10/2012
sl	Female	Adult	-	**22**	Gave birth 22/04/2013
st	Female	Adult	-	**37**	Gave birth 17/10/2012

tr	Female	Adolescent	Adult	**57**	Became adult July 2012. Gave birth 10/01/2013, infant died 07/02 from seemingly natural causes
tu	Female	Adult	-	**50**	Gave birth 23/12/2012
yo	Female	Adult	-	**2**	
ac	Male	Adolescent	Adult	**60**	
adm	Male	Adolescent	-	**12**	
bl	Male	Old Juvenile	-	**23**	
br	Male	Old Juvenile	-	**85**	
ce	Male	Adult	-	**1**	
cr	Male	Old Juvenile	-	**26**	
da	Male	Adult	-	**35**	
dr	Male	Adolescent	N/A	**24**	Emigrated August 2012
ez	Male	Adolescent	-	**1**	
fa	Male	Pubescent	Adolescent	**21**	Became adolescent April 2013
fl	Male	Old Juvenile	-	**66**	
fh	Male	Pubescent	Adolescent	**36**	Became adolescent March 2013
go	Male	Pubescent	Adolescent	**61**	Became adolescent April 2013
jo	Male	Adult	-	**39**	
mc	Male	Adolescent	N/A	**10**	Emigrated March 2013
mt	Male	Adult	-	**2**	
mu	Male	Young Juvenile	-	**1**	
na	Male	Old Juvenile	-	**80**	
ncr	Male	Old Juvenile	-	**9**	
py	Male	Adult	N/A	**24**	Emigrated/died September 2012
pb	Male	Young Juvenile	-	**21**	
ri	Male	Adult	-	**6**	
ro	Male	Adult	N/A	**24**	Emigrated August 2012
sx	Male	Adolescent	-	**9**	
sp	Male	Old Juvenile	Pubescent	**87**	Became pubescent February 2013
tu	Male	Old Juvenile	-	**53**	
va	Male	Adolescent	-	**70**	
vl	Male	Old Juvenile	Pubescent	**47**	Became pubescent March 2013
wo	Male	Adolescent	-	**42**	

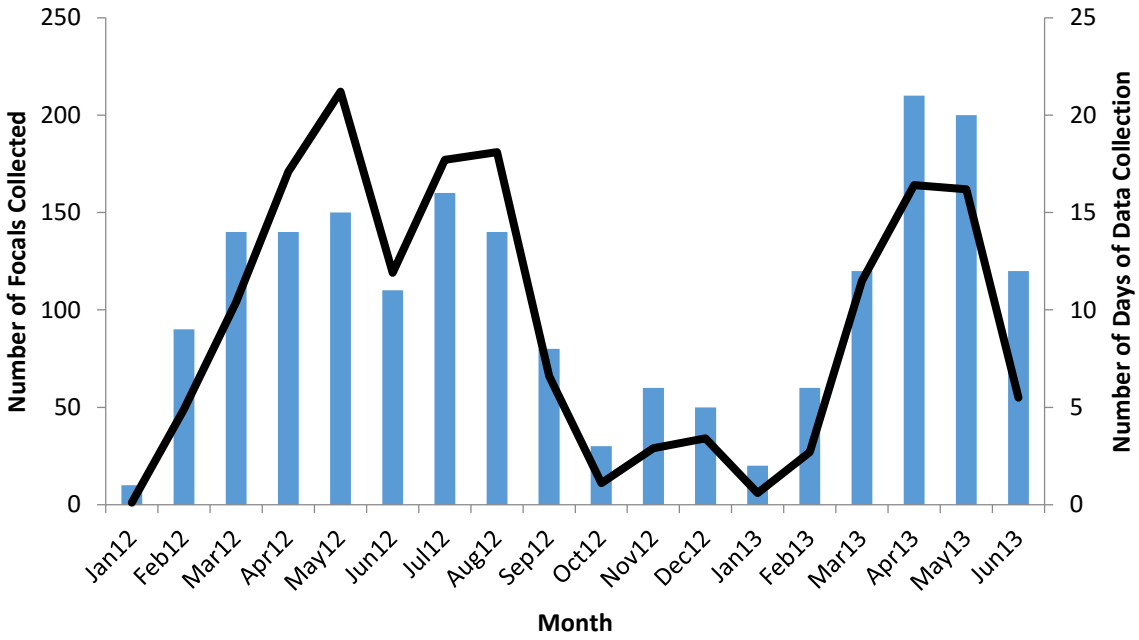

Figure 2.8: Number of focal samples collected per month (black line) and number of days in which data were collected per month (blue columns)

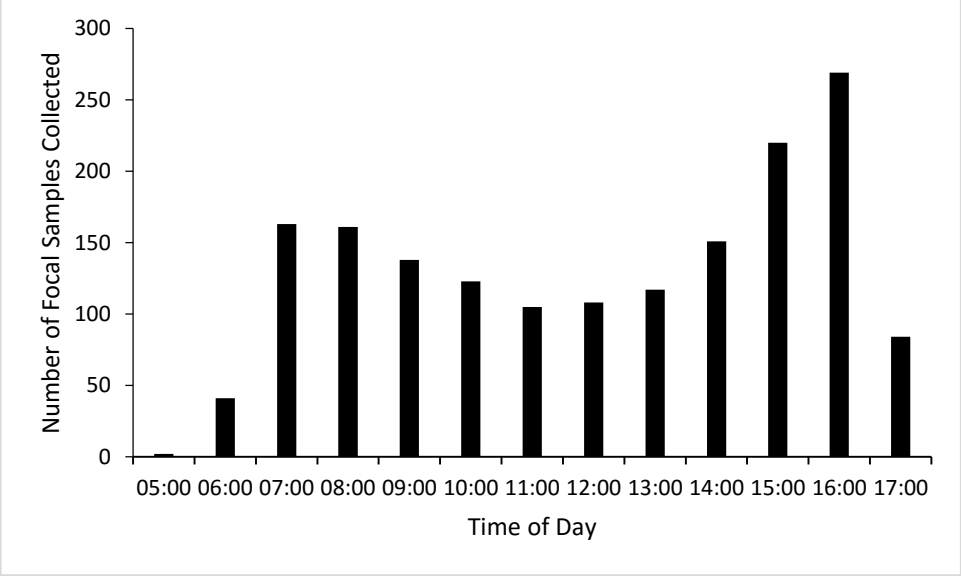

Figure 2.9: Total number of focal animal samples collected in each hour of the day during the study

2.3.3 Ad libitum data collection

In addition to the social information I recorded during my focal samples, I also recorded interactions between individuals as they occurred throughout the day. I also recorded female reproductive states, consortships, emigrations/immigrations, births and deaths daily.

2.2.3 GPS Data collection

During contact with the baboons I used a Garmin 62s set to record coordinates in UTM format every 10 m. I used a distance rather than time-based recording protocol to ensure that step-lengths were equal and evenly spaced, and because of the margin of telemetric error due to the topography (+-3-5 m). In addition to the general path taken by the baboons, I also recorded waypoints at the beginning and end of every focal, and in the centre of the group for each scan.

3 Age and Sex Related Differences in Primate Activity Budgets and Use of Vertical Space

3.1 Introduction

Activity budgets are employed as indirect measures of how animals meet their energetic requirements and as such are expected to reflect physical and socioecological differences between both groups and individuals (Strier 1987). Energetic requirements are considered to be determined by three main factors: the costs of baseline functions (Basal Metabolic Rate, BMR), the costs of activity, and the costs of specific life stage events (reproduction and lactation for adult females, and growth for juveniles) (Chapman et al 2012). Energetic requirements scale in proportion to body mass, with the absolute metabolic need increasing with size, while the energy required per unit of body weight decreases (Strier 1987). This allometric scaling has been determined as approximately 3/4 of body mass, with BMR calculated as Body Weight x 0.75 (Kleiber 1961), while an additional measure states that the energy needed to maintain life during normal activities (Field Metabolic Rate, FMR) can be calculated as 4.63 x Body Weight x 0.762 (Nagy and Milton 1979).

Energetic intake is determined by food availability and foraging success and like energetic expenditure is expected to reflect physical and socioecological differences between both groups and individuals. In primates, sex differences in feeding behaviour have been reported in many species (Clutton Brock & Harvey 1977), with the major differences being that females spend more time foraging than males and or consume more protein-rich foods (Rose 1994). Age differences have also been observed, with juveniles spending more time feeding relative to predictions based on energetic requirements alone (Janson & van Schaik 2002), indicating a degree of foraging incompetence (*ibid*). Juvenile primates may require more time to process foods (Post et al 1980) meaning that for every unit of time spent feeding they ingest fewer calories than adults. Juveniles may also exhibit differences from adults in the amount of time spent feeding on certain food classes (Harrison 1983).

Most primates spend up to 95% of their time engaged in one of four major activities, feeding, moving, socialising and resting (Dunbar 1988, Dunbar 1992), with the time allocated to these activities differing by age-sex class reflecting different behavioural and nutritional priorities (van Noordwiijk et al 2002). Time has long been seen as an important constraint affecting primate activity (Dunbar 1992) and animals in general need to make compromises in the proportion of time allocated to the different activities while still maintaining calorific intake and predator avoidance strategies (Lima 1987, 1988). These compromises are largely dependent on food availability (and therefore seasonality), with primates exhibiting behavioural flexibility when food is scarce, such as reducing group size, travelling for longer distances, or simply reducing activity (Ganzhorn et al 2003).

Primates are highly social animals and social activities are integral for maintaining group stability and cohesion (Lehman et al 2007, Schino 2007). Primate groups are characterised by a high degree of social grooming, which, in addition to having a practical function of removing ectoparasites, also maintains bonds between individuals and alleviates stress and tension (Terry 1970, Dunbar 1991) particularly among female group members in matrilocal groups (Henzi & Barratt 1999). Additionally, play behaviour is ubiquitous in younger primates, with a proposed ultimate function of the acquisition and enhancement of skills vital to adult success (Poirier & Smith 1974, Owens 1975) and enjoyment providing a proximate mechanism to promote this (Bekoff 2001). Play behaviour tends to decrease as primates mature, with peaks of play in infancy and young juvenility being replaced by more adult behaviours until play is virtually absent (Fagen 2002). Despite the importance of social behaviours, time spent engaging in them is sensitive to the environment. Play behaviour in juveniles is reduced in times of nutritional stress and low food availability (Lee 1984, Stone 2008), while grooming in adults declines in poor habitats relative to rich habitats (Lehmann et al 2007).

In addition to the general differences in activity between age-sex classes, there may also be differences in where they undertake these activities. Predation risk can be affected by how visible an individual is to a predator therefore the use of refuges or covered

areas is a potential factor in age-sex class differences. Juveniles are expected to take fewer risks than adults to maximise survival to adulthood (Jansen & van Schaik 2002, Fitchel 2012), and studies have shown that juveniles avoid open habitats more than adults (Fragaszy 1990) or forage less often in higher risk areas (Stone 2007).

While terrestriality and subsequent adaptations are significant in some Old World Primates, notably savannah baboons (*Papio* spp) and geladas (*Theropithecus*) (McCrossin et al, 1998), most primates live in a three-dimensional arboreal space (Kimura 2002). The proportion of time spent at different heights above the ground differs by age-sex class, with juveniles spending greater time above the ground (e.g. Barbary macaques (*Macaca sylvanus*) Menard 1985, long-tailed macaques *(Macaca fasicularis*) Noordwijk et al 2002). Several studies have indicated that the use of vertical space in primate groups is strongly related to body size, with both accessibility of resources on precarious branches and exposure to predators being key aspects of trade-offs in relation to resource acquisition at elevated levels or on terminal branches (Menard 1985, Menard & Vallet 1986, Janson & van Schaik 2002).

Juveniles' small body size allows them access to resources that larger bodied adult individuals may not be able to use, primarily tree-based resources (Menard 1985). However, this same small body size may also make them more prone to predation risk, particularly from airborne predators (Stone 2007). Immature primates have a far higher rate of mortality through predation than adults (Janson & van Schaik 2002), although selective predation on immature individuals remains largely undocumented (Cords 2012). Even where documented, this selectivity is equivocal. For example, while a longitudinal study of predation on monkeys by crowned hawk eagles (*Stephanoaetus coronatus*) found a prey preference for infant and juvenile red colobus (*Procolobus badius*), adult males were preferred in four other monkey species (Struhsaker and Leakey 1990). Potential predators of primates exhibit marked interindividual variation in prey preference (e.g. leopards (*Panthera pardus*): Zuberbuhler & Jenny 2002), and the risk of predation from different classes of predator varies according to height (Seyfarth et al 1980). The extent of terrestrial and non-terrestrial space use by different age-sex classes may provide insights into anti-predation strategies. While being high up in trees

may allow smaller individuals to feed on resources relatively free of within-group competition from larger group members, in doing so they may lose the protection from predators that these larger group members may provide.

Chacma baboons are among the most sexually dimorphic of the cercopithecines, with adult males weighing approximately twice as much as adult females (Cords 2012). Baboons exhibit slow growth early in development, and while female growth rates gradually decline until adult body weight is achieved, males undergo accelerated growth in adolescence (Pereira & Leigh 2003). While females have additional metabolic costs relating to reproduction, as males exceed a threshold of being >60% more massive than females their additional energetic costs due to dimorphism exceed those for females (Key & Ross 1999, Chapman et al 2012). Examining the time spent engaged in activities and the use of vertical space in juveniles and adults is important in assessing the different needs and priorities of such heterogenous individuals within a single group.

Aims and Objectives

In this chapter I will examine age and sex class differences in the time allocated to activities and the use of vertical space in a free-ranging group of chacma baboons (*Papio hamadryas ursinus*). I hypothesise that activity budgets and the extent of vertical space in baboons will differ by age and sex as a result of their different behavioural priorities. I test the following predictions relating to feeding behaviour, social behaviour, and the use of vertical space:

1) Due to their inexperience at acquiring and processing food, younger animals will spend a greater proportion of their time engaged in subsistence related activities.
2) As baboons are a highly social species, there should be no difference in the proportion of time sent engaged in social activities between the ages. However, the types of social behaviour individuals engage in will be affected by age, with younger individuals engaging in more play behaviour than older individuals.

3) Younger, and therefore smaller, individuals will spend a larger proportion of their time above the ground than older and larger individuals.
4) Younger individuals will spend more time engaged in feeding activities above the ground as they are smaller and therefore more able to exploit food resources at higher elevations.

3.2 Methods

3.2.1 Study site

I collected data over 19 months (November 2011 - June 2013) at Lajuma Research Centre in the Soutpansberg mountains of the Limpopo Province of South Africa (29°26'05''E, 23°02'23''S). Further details of the study site can be found in the Methods chapter.

3.2.2 Subjects

I collected data on members of House Troop, which has been the focus of intermittent observation since habituation began in 2001 (de Raad 2011, Howlett 2014). Group size fluctuated during the study period from approximately 74 to 80 individuals as a result of births, migration and mortality. Further details on the study group can be found in the Methods chapter.

3.2.3 Data Collection

I collected data via instantaneous scan sampling (Altmann 1974, Martin and Bateson 1993). Scans were conducted at 30 minute intervals, commencing on the first hour or half-hour on encountering the baboons and continuing until either the baboons were out of sight or were nearing their sleeping sites. During each scan sample I recorded the activity and height above ground (Table 2.2, Methods chapter) of as many baboons as possible in a 5 minute sampling period using a Walkabout Psion Pro PDA equipped with

a spreadsheet programme (SpreadCE). Due to the time intensive nature of attempting to individually identify each baboon in a complex environment, I collected data at an age-sex class level. As it was also often difficult to accurately determine the sex of juvenile individuals during samples, I only collected data on juveniles at an age class level, while for adolescents and adults I also recorded the sex.

3.2.4 Data Selection

I collected a total of 1,068 scans comprising 12,627 records. I excluded records collected in 5 months (November 2011, October and December 2012, and January and February 2013) from analysis due to problems with data collection (see Methods Chapter). I also excluded data on infants as their behaviour cannot be treated as independent of their mothers, and because they engage in behaviours restricted to their own age classes (ventro-ventral and ventro-dorsal clinging and suckling). I therefore present data for 14 months, resulting in a sample of 1,033 scans with 10,486 behavioural observations.

For each of the 14 months, I calculated the proportion of time spent engaging in each activity as a total of all observations for that age and sex class in that month. Additionally, for those behavioural categories which include subcategories (e.g. Feeding = Food item, Social = Social type), I calculated the proportion of time spent engaging in each subcategory as a proportion of the total time in that category. I also calculated the proportion of time spent at the different heights above or on the ground in the same manner. Finally, I calculated the proportion of time allocated to each of the main behavioural categories that took place on the ground, or above the ground.

3.2.5. Data Analysis

I tested all dependent variables for each age and sex class for normality. In the majority of cases data for the major behavioural categories were normally distributed (Kolmogorov-Smirnoff $p>0.05$), with exceptions being the proportion of time that young juveniles and adult females spent moving, and the proportion of time spent socializing

by older juveniles. For the proportion of time spent at different heights above the ground, again the majority of cases were normally distributed, with the exception of the time that older juveniles spent on the ground and at between the ground and 2 m, the time that adult males spent at 2-5 m, the time that adolescent females and pubescent males spent at 5-10 m, while for the time spent above 10 m all but adult females were not normally distributed. A similar pattern emerged with the proportion of time allocated to each activity on the ground or above the ground. As the majority of data were normally distributed I used parametric tests, which are relatively robust against minor violations of normality (McDonald, 2014).

To test the predictions of age and sex related differences in activity, I conducted one-way ANOVAs to determine whether there were differences in the proportion of time that each age-sex class engaged in each activity, the time spent at different heights, and time engaged in each activity on the ground and above the ground. Where the variances were not homogeneous, I used the Welch test. Where I found a significant result, I used post-hoc pairwise comparisons to determine which groups differed, using Tukey's HSD test where variances were homogeneous, and the Games-Howell test if they were not.

As the majority of behavioural subcategories were positively skewed, I used non-parametric Kruskall-Wallis tests to test for age-sex differences between behavioural subcategories.

I conducted all statistical tests using SPSS 22.0. Statistical significance was set at $p<0.05$ for all tests, with all tests being two-tailed where applicable.

3.3 Results

3.3.1 Activity budget by age-sex class

I found several differences in the proportion of time spent resting, socialising and travel feeding across age-sex classes, but no differences in the proportion of time spent either feeding or moving (Figure 3.1, Table 3.1). All of the pairwise differences relating to the time spent resting involve adolescent and adult males resting more than other age and

sex classes. For the proportion of time spent socialising I found only one difference, between adolescent males and adolescent females. Finally, adult females spent more time foraging than other age sex classes.

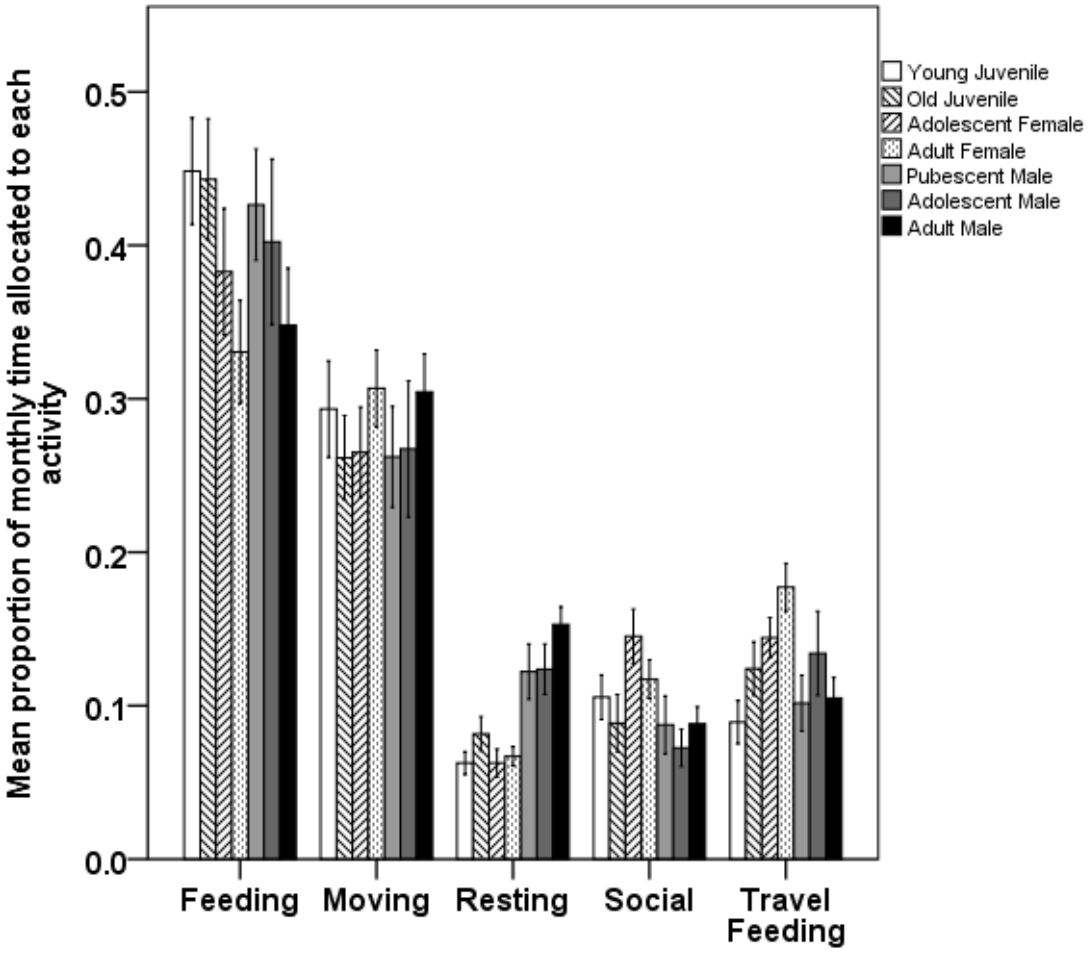

Figure 3.1: Mean +- SE monthly proportion of time engaged in the five major activities for each age-sex class.

Table 3.1: Results of ANOVAs comparing the proportion of time spent engaged in major activity components across age-sex classes, and associated significant post-hoc pairwise comparisons.Significant differences are in bold

Activity	ANOVA	p	Post-hoc comparisons
Feeding	F(6,91)=1.317	0.258	N/A
Moving	F_{Welch}(6,40.334)=0.500	0.799	N/A
Resting	**F_{Welch}(6,39.940)=10.002**	**<0.001**	Games-Howell: Young Juv < Adolescent ♂, p=0.041 Young Juv < Adult ♂, P<0.001 Old Juv < Adult ♂, P<0.003 Adolescent ♀<Adolescent ♂, p=0.049 Adolescent ♀ < Adult ♂, p<0.001 Adult ♀< Adult ♂ , p<0.001
Social	**F(6,91) =2.493**	**0.020**	Tukey's HSD: Adolescent♂<Adolescent ♀,p=0.020
Travel Feeding	**F(6,91) =2.876**	**0.013**	Tukey's HSD: Young Juv < Adult ♀, p=0.012 Pubescent ♂ < Adult ♀ p=0.049

For the activities that contained behavioural subcategories (feeding, resting, and social activities), I only found differences between age-sex classes in the proportion of time spent engaging in three social activities: allogrooming, playing and sexual activities (Table 3.2).

Table 3.2: Kruskall-Wallis tests for the proportion of time spent engaging in behavioural subcategories by age and sex class. d.f = 6 for all tests

Activity	Subcategory	Kruskall-Wallis (H)	p
Feeding	Drinking	9.413	0.152
	Animal	3.712	0.716
	Other	7.656	0.264
	Leaves	6.368	0.383
	Grasses	1.583	0.954
	Digging	0.396	0.999
	Fruit	3.020	0.806
Resting	Covered	6.442	0.376
	Exposed	" "	" "
Social	**Allogrooming**	**30.472**	**<0.001**
	Playing	**50.555**	**<0.001**
	Sexual activities	**18.375**	**0.005**
	Aggression	10.120	0.120
	Autogrooming	4.972	0.547
	Huddling	3.869	0.694
	Other	9.193	0.163

All age and sex classes fed almost exclusively on fruits and seeds, subterranean food items and grasses, with these categories comprising from 86.8% of older juveniles' diets, to 92.4% in adult males (Figure 3.2).

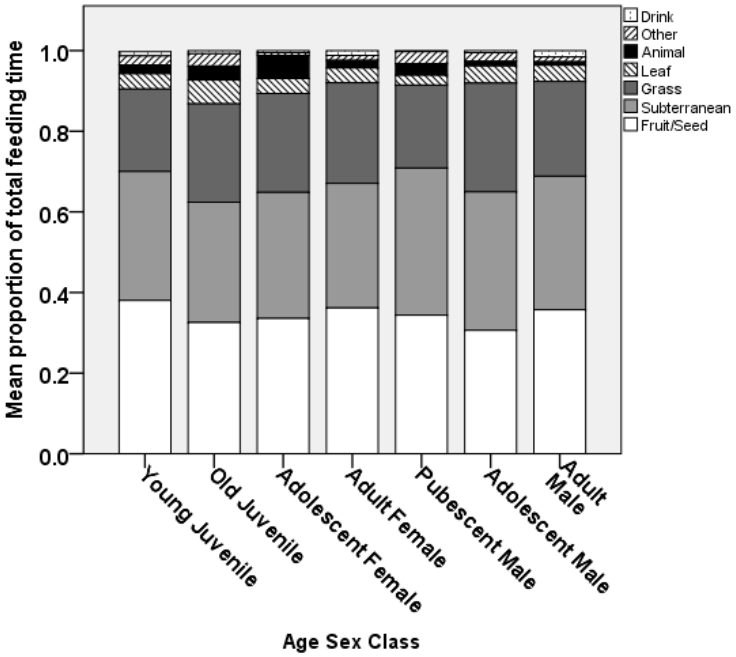

Figure 3.2. Time spent feeding on each item as a proportion of total time spent feeding by age-sex class

Of social behaviours (Figure 3.3), allogrooming was the most prevalent activity in all age-sex classes with the exception of the youngest juveniles who spent more of their social time playing, an activity virtually absent in older classes. Meanwhile, sex-related behaviours were least common in the reproductive age-sex classes (adult females, adolescent and adult males), and highest in three of the non-reproductive classes (adolescent females, old juveniles and pubescent males).

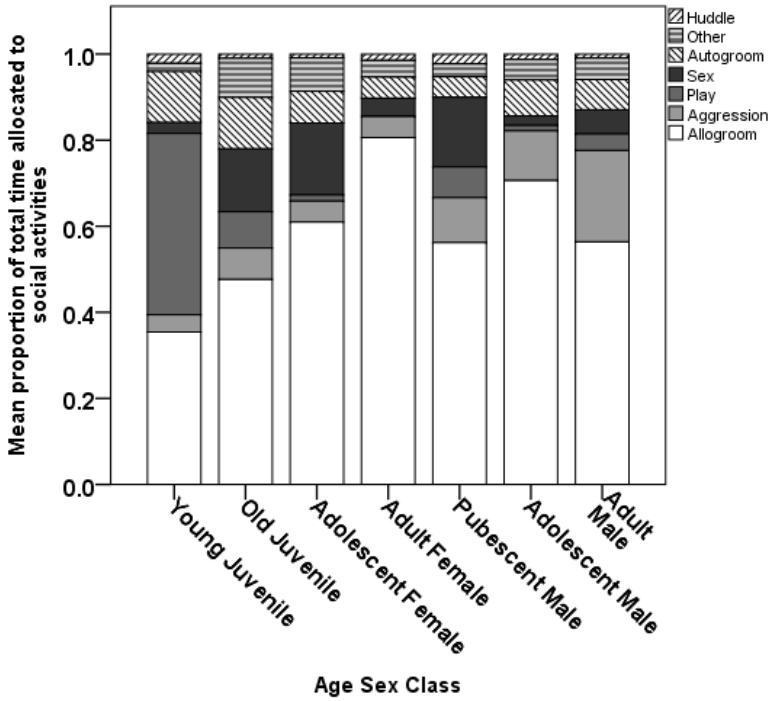

Figure 3.3. Proportion of time spent engaged in each social activity as a percentage of total time spent socializing by age-sex class

3.3.2 Time spent at different Heights

I found several differences in the proportion of time spent at each height (Figure 3.4, Table 3.3), although all age and sex classes were predominately terrestrial and rarely spent any time at greater than 5 m above the ground. The youngest juveniles spent less time on the ground than adolescents and adolescent of both sexes, and also spent more time 2-5 m above the ground than adults of both sexes.

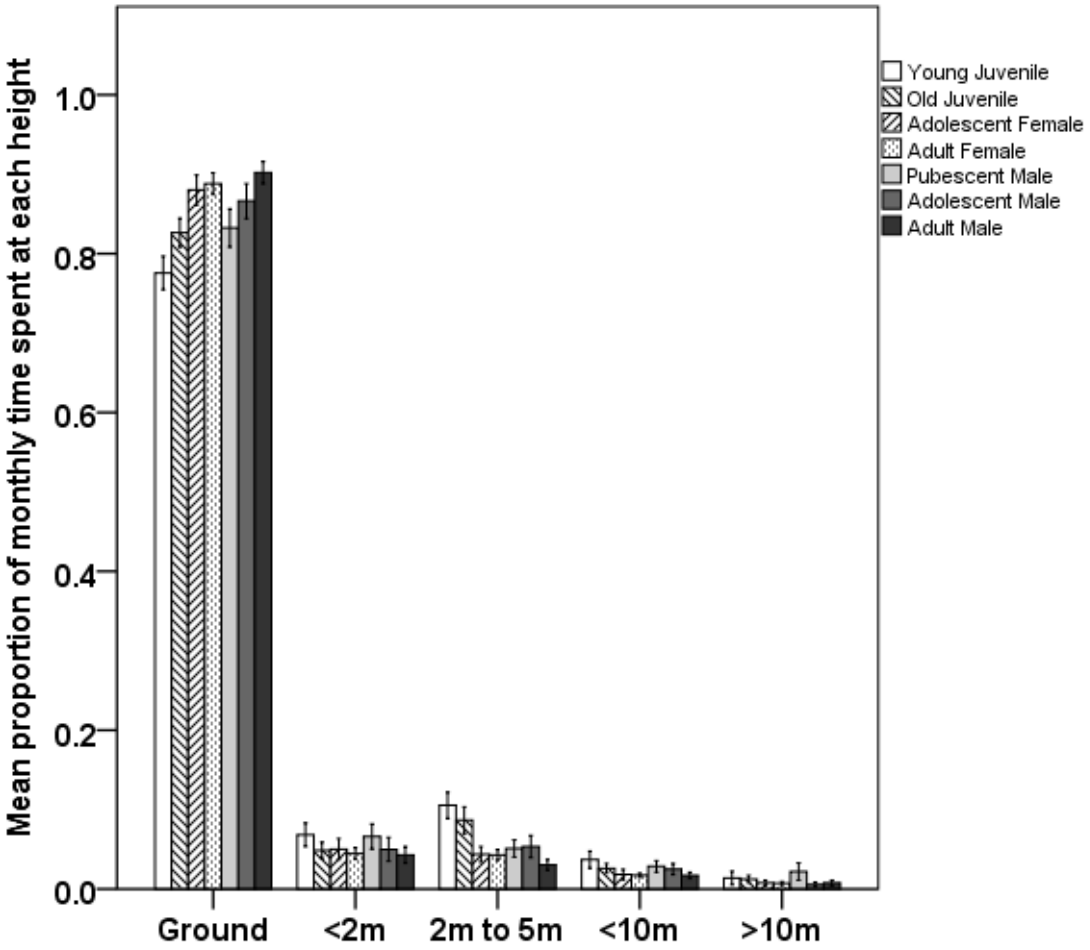

Figure 3.4: Mean +- SE monthly proportion of time spent at the 5 different heights for each age-sex class.

Table 3.3: Results of ANOVAs comparing the proportion of time spent at each height across age-sex classes, and associated significant post-hoc pairwise comparisons.Significant differences are in bold

Height	ANOVA	p	Post-hoc comparisons
Ground	**F(6,91) = 5.334**	**<0.001**	Tukey's HSD: Young Juv < Adolescent ♀, p=0.004 Young Juv < Adolescent ♂, p=0.019 Young Juv < Adult ♀, P<0.001 Young Juv < Adult ♂ , p<0.001
< 2 m	F(6,91) = 0.636	0.701	N/A
2 – 5 m	**F_{Welch}(6,39.907) = 3.875**	**0.004**	Games-Howell: Adult ♂ < Young Juv, p=0.008 Adult ♀ < Young Juv, p=0.034
5 – 10 m	F_{Welch} (6,39.347)= 1.098	0.381	N/A
>10 m	F_{Welch} (6,39.830)= 0.574	0.749	N/A

3.3.3. Activity at Different Heights

I found several differences between age-sex classes between the proportion of time spent engaged in activities on or above the ground (Table 3.4, Figs 3.5-9). Most of the differences reflect the more general pattern of activity presented in section 3.3.1, with the majority of these differences occurring on the ground as a result of the largely terrestrial habits of the group. While there were no significant differences in the general proportion of time spent feeding between the age and sex classes (section 3.3.1), the proportion of time spent feeding above the ground was significantly different. The youngest juveniles spent more of their time feeding above the ground than adolescents or adults of both sexes.

Table 3.4: Results of ANOVAs comparing the proportion of time engaged in each activity on the ground or above the ground across age-sex classes, and associated significant post-hoc pairwise comparisons.. Significant differences are in bold.

Activity	ANOVA	p	Post-hoc comparisons
Feeding	F(6,91) = 0.429	0.858	N/A
>Ground	**F(6,91) = 4.326,**	**0.001**	Tukey's HSD: Adolescent ♀< Young Juv, *p*=0.032 Adolescent ♂<Young Juv *p*=0.012 Adult ♀<Young Juv *p*=0.006 Adult ♂<Young Juv *p*=0.001
Moving	F_{Welch}(6,40.331)= 0.779	0.591	N/A
>Ground	F_{Welch}(6,40.157) = 1.627	0.165	N/A
Resting	**F_{Welch}(6,40.128)=12.266**	**<0.001**	Games-Howell: Young Juv<Adolescent ♂ *p*=0.022 Young Juv<Adult ♂ *p*<0.001 Old Juv<Adult ♂, *p*<0.001 Adolescent ♀<Adolescent ♂, *p*=0.022 Adolescent ♀<Adult ♂, *p*<0.001 Adult ♀ < Adult ♂, *p*<0.001
>Ground	F_{Welch} (6,39.538)= 1.063	0.342	N/A
Social	**F(6,91) = 2.902**	**0.012**	Tukey's HSD : Pubescent ♂<Adolescent ♀, *p*=0.036 Adolescent ♂<Adolescent ♀, *p*=0.01
>Ground	F(6,91) = 0.659	0.683	N/A
Travel Feeding	**F(6,91) = 3.317**	**0.05**	Tukey's HSD: Young Juv < Adult ♀, *p*=0.002 Pubescent ♂ < Adult ♀, *p*=0.027
>Ground	**F_{Welch}(6,37.833) = 2.841**	**0.022**	N/A

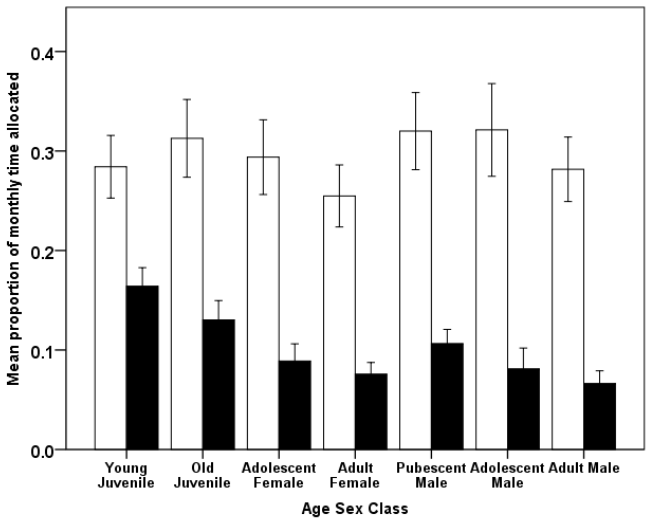

Figure 3.5: Mean +- SE proportion of time spent feeding at ground level (white bars) or above ground level (black bars) by age and sex class

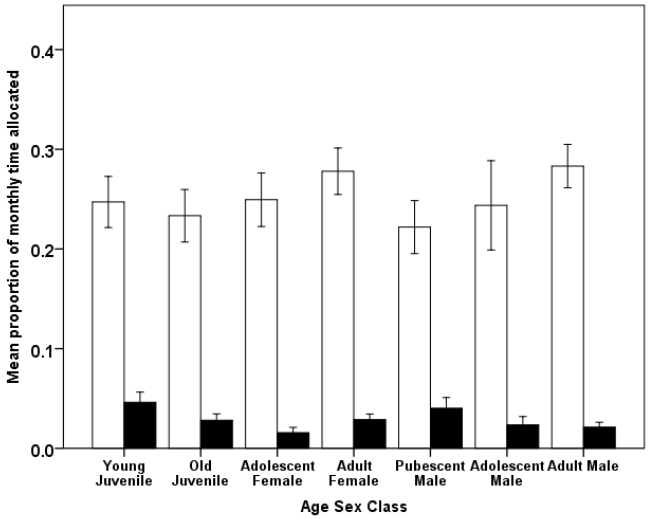

Figure 3.6: Mean +- SE proportion of time spent moving at ground level (white bars) or above ground level (black bars) by age and sex class

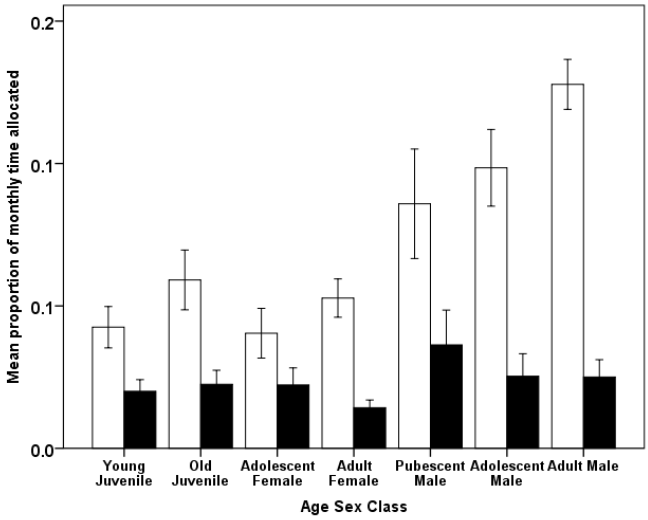

Figure 3.7: Mean +- SE proportion of time spent resting at ground level (white bars) or above ground level (black bars) by age and sex class

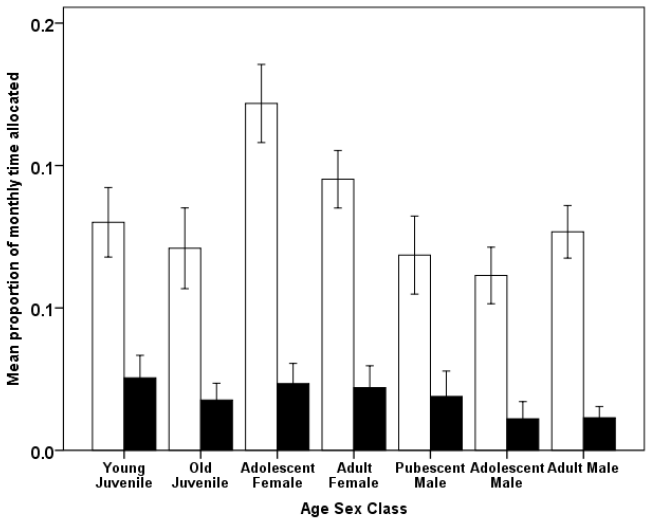

Figure 3.8: Mean +- SE proportion of time spent socializing at ground level (white bars) or above ground level (black bars) by age and sex class

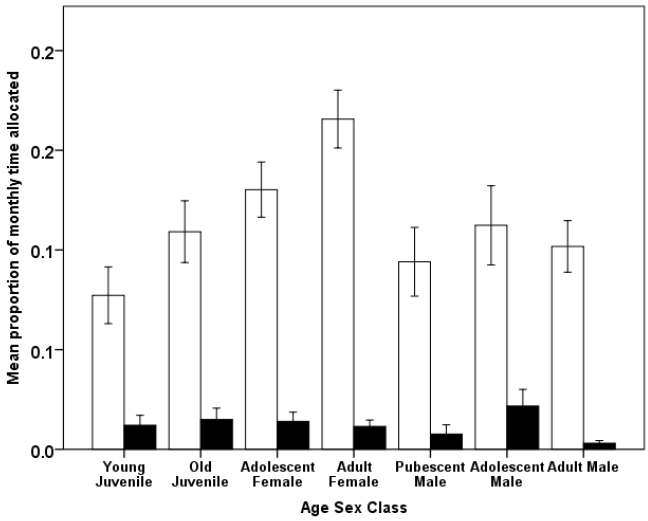

Figure 3.9: Mean +- SE proportion of time spent travel feeding at ground level (white bars) or above ground level (black bars) by age and sex class

3.4. Discussion

In this chapter I assessed the extent to which the general activity of group members varies by age, sex and body size, and whether or not they vary in their use of vertical space. My results indicate that there are indeed differences in the scheduling of activity, time spent at different heights, and the activities engaged in at different heights between the age and sex classes. While my predictions relating to activity budgets are generally not supported, those relating to the use of vertical space are more supported.

While I predicted that the time spent feeding would be highest in juveniles, the results show little support for this with no statistically significant differences between the age sex classes. Considering the underlying relationship between energetic requirements and body size (Strier 1987), the fact that the time spent feeding did not vary by age and sex runs contrary to the juvenile risk hypothesis of the evolution of the primate juvenile period (Janson & van Schaik 2002). However, although I found no statistically significant difference in the amount of time spent feeding by juveniles and adult members of the group, the juvenile classes allocated 135% of the time of adult females, and 129% of the time as adult males to feeding, very similar to previous reports of 132% and 134% respectively in *Papio cynocephalus* (Post 1980). Additionally, I found no differences in the proportion of time feeding on the different food items, indicating significant dietary overlap between individuals of all ages and sex.

. As predicted, the time spent engaged in social activities varied little between the age and sex classes. However, the types of social behaviours engaged in did differ by age and sex,with the social activities of the different age and sex classes reflecting their different social and behavioural priorities. Play was highest in the youngest juveniles, and declined with age until virtually absent in adult males, a similar pattern to that reported elsewhere (Owens 1975, Fagen 2002). With the exception of these young juveniles, grooming was the most prevalent social activity for all age and sex classes. Levels of grooming were highest in adult females, similar to previous findings that social grooming is a predominantly female activity (Mitchell & Tokunaga 1976, Seyfarth 1977, Thierry et al 1990, Henzi & Barratt 1999). Meanwhile, the proportion of time engaging in sexual activity saw a peak in adolescent females, and was higher in juveniles than in adults. As adult males tended to ignore sexual solicitations by adolescent females, the heightened sexual activity in adolescent females was almost exclusively due to copulations with juvenile males (personal observation).

Baboon activity budgets are known to vary widely in relation to seasonal and environmental conditions, with baboon groups exhibiting high degrees of behavioural flexibility (Dunbar 1992, 1996, Hill et al 2004, Hill 2006, Ross et al 2011). The activity budgets found in the adult population of my study group fall somewhat outside the ranges found in such comparative studies relative to other chacma baboon studies (i.e.

Whiten et al 1987, 1991, Hill 1999, Barrett et al 2006). While I chose to use five components in activity budgets, placing travel feeding as a separate category outside both feeding and travel behaviour, if incorporated into feeding, the population at Lajuma appears to spend more time feeding (48% of their time relative to a range of 34-40%, Ross et al 2011),and less time resting than other populations (11% of the time, relative to a range of between 16-21%), although similar amounts of time both moving (31% relative to a range of 29-31%) and socialising (10% relative to a range of 11 to 13%). This may be an artefact of removing months with few data from my analyses (November 2011, October and December 2012, and January and February 2013). These months are seasonally characterised by elevated NDVIs and food availability at the study site (Willems 2007, Willems et al 2009), meaning that the data I present may preclude effective comparisons with other baboon studies, and caution is therefore needed in interpreting the activity budgets I report within a wider context.

The results for the use of vertical space follow my predictions, with the youngest, smallest individuals spending less time on the ground than older individuals. While adult males were almost exclusively terrestrial, smaller individuals spent more time above the ground, with the youngest juveniles being less than 80% terrestrial. While no age-sex class spent a large proportion of their time at any height greater than 10m, and there were no differences in the time spent between the ground and 2m, the youngest juveniles spent significantly more time than any other age-sex class at 2-5 m. Young juveniles may therefore be more able to use resources or refuges above the ground that older individuals are less capable of accessing (Menard 1985, Menard & Vallet 1986). That the youngest juveniles spent more at elevated positions than older individuals is contrary to the prediction that smaller animals will be more susceptible to predation from airborne predators (Janson & van Schaik 2002, Stone 2007), and will therefore avoid such areas. Selective predation on immatures is still relatively undocumented (Cords 2012), and despite the presence of several species of raptors at the study site, the only evidence for predation by raptors I observed was an infant dying from injuries as a result of a suspected failed eagle predation event. This population may therefore be able to use vertical space and exposed or terminal branches with very little risk of predation. Furthermore, by spending more time at elevated heights younger animals

may also be protecting themselves against the risk of predation by more terrestrial threats, particularly in relation to leopards (*Pantera pardus*) and rock pythons (*Python sebae*).

Similarly, my prediction that young juveniles would spend more time feeding above the ground than older, larger individuals was supported. The youngest juveniles spent significantly more time feeding above the ground than either adolescents or adults of both sexes. Considering that no differences were found in the total amount of time spent feeding, the fact that a significant difference emerges when examining feeding behaviour on or above the ground indicates that there may be a degree of niche separation between younger and older individuals (e.g. Janson & van Schaik 2002). Over a third (~37%) of the youngest juveniles' feeding activity took place above the ground, far higher than adult females (~25%) or adult males (~20%). It is possible that the youngest juveniles are thus able to protect themselves against within-group feeding completion through their access to arboreal food sources that older, larger individuals are less able to acquire.

The majority of significant post-hoc comparisons for activity budgets involve differences between adolescent and adult males and the other age sex classes, while differences related to the time spent at heights above the ground are restricted to differences between the youngest juveniles and adolescent and adult males and females. An important finding of this study is that there were no differences in either activity or the use of vertical space among any of the juvenile classes (young and old juveniles and pubescent males), or between any of the same-sex adolescent and adult classes, indicating that adolescent and adult individuals of both sexes are comparable with one another. Effectively, by adolescence baboons exhibit the same activity profile as adults, with adolescent males being most similar to adult males, and adolescent females being most similar to adult females. However, this study is limited by the fact that juveniles were not identified by sex, both through difficulty in sexing individuals in rapid scan sampling, but also because there were often no female individuals of the older juvenile class, while pubescence is a male only class.

Sex-specific differences in activity budgets may emerge before adolescence in baboons, and although numerous studies have focused on sex-biased differences in social behaviour and its development in juvenile primates (e.g. Wolfheim 1977, Eaton et al 1986, Pereira 1989), few have examined sex differences in general behavioural ecology (e.g. van Noordwijk et al 1993). Indeed, it is common to group juveniles by size rather than by sex (e.g. O'Brien and Kinnaird 1997) or just as juveniles as a sub-class in itself (e.g. Saj et al 1999). Several studies have shown that male and female growth-rates, and therefore body size, are equivalent in baboons until approximately 5.5 - 6 years of age (Altmann & Alberts 1987, Johnson 2003), and males and females are therefore expected to have similar basal nutritional and calorific requirements. At this age females are likely to be reproductively active, while males undergo their adolescent growth spurt, at which point their requirements will diverge.

3.5. Conclusion

Although activity budgets are well studied at a group-level (e.g. meta-analyses for baboons conducted by Dunbar 1992, Dunbar et al 2009, Hill & Dunbar 2002), few studies examine individual variation in primate activity budgets (Marshall et al 2012). This means there is a paucity of information on age and sex related variation in activity patterns. My findings indicate that there are important differences in how baboons of different ages and sexes schedule their activities, and where they conduct these activities. Although I found no age and sex differences in the total amount of time spent feeding, young juveniles spend significantly more time feeding above the ground than older, larger individuals. Older, larger animals are more terrestrial, which may allow young juveniles to reduce the risk of within-group competition by feeding higher up in areas less accessible to adults. Additionally, while there were no significant differences in the proportion of time allocated to social activities, there were significant differences in the types of social activities they engaged in reflecting their different social priorities. The most frequent social activity for young juveniles was playing, while social grooming was the most common activity for all other classes, particularly adult females. In the next chapter, I examine the extent to which immature and mature individuals are engage in the same activities at the same time.

4. Behavioural Synchrony in Non-Human Primates

4.1. Introduction

Group-living is common across animal species, ranging from temporary aggregations formed in relation to feeding or reproduction to the permanent multi-generational colonies found in the eusocial Hymenoptera and Isoptera (Plowes 2010). Individuals of solitary species form groups around food resources (e.g., *Ciconiiform* wading birds, Kushlan 1981) orang-utans (*Pongo pygmaeus*, Utami et al 1997), *Macropodes* spp. (Nowak 1999), while other species form leks for mating (e.g., natterjack toad (*Bufo calamua*), fallow deer (*Dama dama*) (Fiske et al 1998)). In societies with high fission-fusion dynamics variation in spatial cohesion and group membership is commonplace, often involving temporary splitting of sub-groups from the parent group (e.g., African elephants (*Loxodonta Africana*), bottlenose dolphins (*Tursiops* spp.), chimpanzees (*Pan troglodytes*), hamadryas baboons (*Papio hamadryas*), spotted hyena (*Crocuta crocuta*) Aureli et al 2008).

Several benefits are proposed for group-living, including decreased individual or group predation risk (e.g., woodpidgeons (*Columba palmbus*), Kenward 1978; Alaskan moose (*Alces alces gigas*), Molvar & Bowyer 1994; Cercopithecoid primates, Hill & Lee 1998), increased hunting success in communal carnivores (e.g., wild dogs (*Lycaon pictus*) Creel & Creel 1995) or opportunistic primates (e.g., chimpanzees (Boesch 1994), and increased foraging efficiency either through information exchange (Clutton-Brock 1974, Galef & Giraldeau, 2001) or the communal defence of food sources (Wrangham 1980).

There are also costs associated with communal living, particularly with regards to resource acquisition. For example, as group size increases, the daily distance travelled and the amount of time spent feeding increases in primates as a consequence of intragroup competition (Majolo et al 2008). Increasing group size is also associated with both an increased prevalence and intensity of contagious, but not mobile, parasites (Cote & Poulinb 1995), while increasing variability in group size can reduce the epidemic

threshold for disease transmission, making populations more susceptible to pathogens (Caillaud et al 2013).

Group-living will evolve if the benefits outweigh the costs (Majolo et al 2008), although there are constraints on maximum group size. Several studies have indicated that there are maximum ecologically tolerable group sizes beyond which groups are no longer sustainable on the basis of time and resources available to members (Chapman 1990, Dunbar 1992, Chapman & Chapman 2000a,b, Hill et al 2003). There may also be cognitive restraints on the maximum size of a group, as proposed in the Social Brain Hypothesis (Barton and Dunbar 1997, Dunbar 1998), based on the consistent relationship found between primate group size and primate brain size (e.g. Dunbar 1992, Kudo and Dunbar 2001).

Behavioural synchrony is defined as individuals engaging in the same activity at the same time (Engel & Lamprecht 1997, Raussi et al 2011, Asher & Collins 2012), and is an important aspect of living in a group (Ruckstahl 1999). To obtain the benefits afforded by group-living, animals must move together as a unit, and coordination is required to avoid moving and foraging independently and becoming separated from the rest of the group (King & Sueur 2011). Coordination of behaviour, and therefore the extent of behavioural synchrony of an individual with other group members, may entail a compromise, particularly with regards to activity budgets (Conradt & Roper 2000). For example, an individual may want to remain at a feeding site, but if the rest of the group move away, it has to sacrifice time spent feeding to remain with the group. It is therefore likely that increased inter-individual competition through individual self-interest as a consequence of group-living is constrained by the trade-off that individuals face in relation to group cohesion (Kappeler 2011).

Animals which are similar in size have similar metabolic costs of activity, and are predicted to have high levels of behavioural synchrony (Aiwaz and Ruckstuhl 2011). Conversely, animals that are dissimilar in size have different nutritional and metabolic requirements and are predicted to have low levels of behavioural synchrony (ibid). This may underlie sexual segregation and the development of bachelor groups, particularly

among species which exhibit a high degree of sexual dimorphism (e.g., in ungulates, Ruckstuhl 1998; Conradt 1998; Michelena et al 2006). Primates exhibit a higher degree of sexual dimorphism than mammals in general (male body size 1.25 greater than females in Primates versus 1.18 in mammals, Lindenfors et al 2007). However, although some primate species form bachelor groups (e.g., proboscis monkeys (*Nasalis larvatus*) Bennet & Sebastian 1988; Hanuman langurs (*Semnopithecus entellus*) Rajpurohit et al 1995), the majority of primate societies are composed of groups with ≥3 adults of mixed sex and their associated offspring (Kappeler & van Schaik 2002).

Studies of behavioural synchrony in primate groups have found that synchrony is generally low (Oates 1986). For example, around half the group were inactive during the peak of red colobus (*Procolobus badius*) feeding bouts (Clutton-Brock 1974), and feeding synchrony in tantalus monkeys (*Chlorocebus tantalus*) was only highly synchronized when they fed on a distinctly clumped resource (Kavanagh 1978). The extent of behavioural synchrony in chacma baboon groups is affected by social and environmental factors, including the time of day, reproductive status of the females, the level of cover afforded by the environment, and the general level of group spatial cohesion (King & Cowlishaw 2009).

Primate groups are characterised by strong affiliative bonds between group members, and individuals coordinate their movement using vocalisations (Oates 1986). While studies of savannah baboons show that group movements tend to be led by dominant males (Byrne et al 1990, King et al 2008), a recent study using GPS data determined that movements are characterised more by democratic collective decision making, with hierarchy playing little role in group movement (Strandburg-Peshkin et al 2015; see also Sellers et al 2007 and Stueckle & Zinner 2008 for democractic movement decisions in baboons, and King et al 2011 for individuals moving in response to close social conspecifics departures and local rule-of-thumb decision processes). Regardless of the processes of collective movement, and whether or not such decisions are despotic or democratic, primate groups are able to maintain cohesive groups as they traverse the landscape. There is however wide intraspecific variability in the cohesiveness of primate

groups, with baboons in particular displaying a spectrum from highly cohesive units (e.g. the typical multi-male multi-female groups common to savannah baboons (Swedell 2011) to fission-fusion dynamics (e.g. one-male units in hamadryas baboons (Kummer 1968)) depending on environmental and social factors (Henzi & Barret 2003, Barton et al 1996, Patzelt et al 2011).

Coordination of movements does not mean that general behaviour is synchronised. Group members are unlikely to leave related and vulnerable group members (e.g. juveniles) behind as they travel, and as younger individuals may require more feeding time to meet their calorific requirements (Post 1980, Janson & van Schaik 2002, Chapter 3), older group members which have already met their subsistence needs may engage in other activities. This may account for the elevated levels of grooming in adult females and resting in adult males when compared to younger individuals (Mitchell & Tokunaga 1976, Henzi & Barratt 1999, Chapter 3).

Primates grow slowly compared to other similarly-sized mammals, spending a substantial proportion of their total lifespan at relatively small body sizes compared to adults of both sexes (Kappeler et al 2003). The presence of immature individuals in a primate group may constrain behavioural synchrony as a result of differences in activity budgets between the age and sex classes (Chapter 3). Furthermore, most non-human primates live in a three-dimensional arboreal space (Kimura 2002), and the amount of time spent at different heights varies by age-class and body size (Menard 1985, Chapter 3). Incorporating height above ground into analyses of behavioural synchrony alongside variation in activity between age classes may assist in determining potential niche separation between group members of differing ages, with implications for group behavioural synchrony. No study has addressed the impact of the unique primate life history pattern of prolonged immaturity on behavioural synchrony.

There are multiple methods for measuring synchrony. Some researchers group behaviours into binary *active/inactive* categories (Conradt 1998, Ruckstuhl 1999, Sarova et al 2007), while others include a larger number of behavioural categories (e.g., 6 in King and Cowlishaw 2007, 9 in Foerder et al 2013). Studies of behavioural synchrony are

also conducted on groups of varying size, or using different sampling regimes. A recent review addressed the issue of these potential confounds by testing the correlation between some of the most common methods found in the literature with a simulated synchronization factor (*s*) (Asher & Collins 2012). Using data derived from scan samples of egg-laying hens and altering the number of behavioural categories by grouping related behaviours together (in order of decreasing complexity, 10, 5, 3 and 2 different behavioural categories) and simulating groups sizes between 2 to 300, Asher and Collins compared four commonly used methods for assessing synchrony:

i) Proportion of observations with 100% conforming behaviour

ii) Mean proportion of behaviourally conforming individuals

iii) Ruckstuhl's group mean

iv) The Kappa Coefficient of Agreement (Kappa)

Of these measures, Kappa was the most accurate measure of behavioural synchrony. It is the only measure which controls for expected levels of synchrony, and was less affected by group size than any of the other measures. Asher & Collins also conclude that five behaviours is the optimal number of categories for measuring synchrony, as too many categories may lead to a false negative result of asynchrony, while too few categories may lead to a false positive of synchrony. As these conclusions were derived from simulated data for captive animals, validation from different behavioural and ecological settings can help to further explore the use of Kappa as a tool for assessing behavioural synchrony.

Aims and objectives

In this chapter I aim to examine behavioural synchrony in a free-ranging group of chacma baboons, exploring both demographic and methodological factors. In Chapter 3 I found age- and sex-related differences in activity budgets and the use of vertical space in this group, but no differences between juvenile age-classes, or between same-sex adolescents and adults. In this chapter I partition the data into immature (young and old

juveniles and pubescent males) and mature individuals (adolescent and adult males and females). I first examine the prevalence and distribution of different activities to examine behavioural differences and similarities between these two groups. I then examine behavioural synchrony of the whole group, an immature-only subset, and a mature-only subset. I also examine the effects of using different numbers of behavioural categories and the inclusion of height above ground on the extent of behavioural synchrony. Finally, I examine the effects of group membership on behavioural synchrony to determine the extent of niche separation between the immature and mature groups through randomising the assignation of individuals to either the immature or mature sub-groups. I test four sets of predictions:

1) The proportion of immature and of mature individuals engaged in each activity during a scan will be positively correlated. However, immature and mature individuals will differ in the proportion of time spent engaging in activities in each scan.
2) Behavioural synchrony will be higher in subsets composed of individuals of similar ages, and lower when I include all group members.
3) Behavioural synchrony will decrease as the number of behavioural categories used increases, and that including whether or not an activity took place on or above the ground will decrease values of behavioural synchrony.
4) Randomly assigning individuals to either the immature or the mature sub-group will lead to lower levels of behavioural synchrony than found in groups containing only immature or mature individuals.

4.2. Methods

4.2.1 Study site

I collected data over 19 months (November 2011 - June 2013) at Lajuma Research Centre in the Soutpansberg mountains, Limpopo Province, South Africa (29°26’05’’E, 23°02’23’’S). Further details of the study site are in the Methods chapter.

4.2.2 Subjects

The subjects of data collection were House Troop. Group size fluctuated from approximately 74 to 80 individuals during the study period as a result of births, migration and mortality. Further information on group demography is in the Methods chapter.

4.2.3 Data Collection

I collected data using scan sampling (Altmann 1974, Martin and Bateson 1993) at 30 minute intervals, commencing on the first hour or half-hour on encountering the baboons and continuing until either the baboons were out of sight or were nearing their sleeping site. During each scan, I recorded the activities of as many baboons as possible in a 5 minute sampling period using a Walkabout Pro Psion PDA equipped with a spreadsheet programme (SpreadCE). I collected data at an age/sex class level, using the data collection protocol in Section 3.2.3.

I combined behavioural categories to produce datasets with 2, 5 and 10 behaviour categories, maintaining the mutual exclusivity and exhaustiveness of the ethogram. Combined with height included/height not included (Table 4.1), this led to a maximum of 20 categories.

Table 4.1. Behavioural categories used for behavioural synchrony tests

10 Behaviours	5 Behaviours	2 Behaviours		Height Modifier
Feed subterranean	Feed	Immobile		Ground Not on Ground
Feed Fruit	Feed	Immobile		Ground Not on Ground
Feed Grasses	Feed	Immobile		Ground Not on Ground
Feed Other	Feed	Immobile		Ground Not on Ground
Rest Covered	Rest	Immobile	**X**	Ground Not on Ground
Rest Exposed	Rest	Immobile		Ground Not on Ground
Social Grooming	Social	Immobile		Ground Not on Ground
Social Other	Social	Immobile		Ground Not on Ground
Move	Move	Mobile		Ground Not on Ground
Travel Feed	Travel Feed	Mobile		Ground Not on Ground

4.2.4 Data Selection

I used 889 scans, including 9,784 individual records for analysis. 3,912 were for immatures (young juveniles, older juveniles and pubescent males) and 5,872 were for mature animals (adolescents and adults; Table 4.2). I excluded infants as their behaviour cannot be treated as independent of their mothers, and because they engage in behaviours restricted to their own age class (ventro-ventral and ventro-dorsal clinging and suckling). I also excluded scans containing fewer than 2 immature individuals and/or fewer than 2 mature individuals because a group with zero individuals cannot be synchronised, and a single individual will always be synchronised with itself.

Table 4.2 Descriptive statistics for the number of individuals present in a scan sample

	Range	Minimum	Maximum	Mean (SE)	Std. Error
Mature	17	2	19	6.61 (0.093)	2.777
Immature	11	2	13	4.40 (0.066)	1.962
Total	24	4	28	11.01 (0.122)	3.636

4.2.5. Data Analysis

Prevalence and Distribution of Activities

As the data were not normally distributed (Kolmogorov-Smirnoff $P<0.05$ for all categories), I employed non-parametric tests. The unit of analysis is the proportion of immature and mature individuals time engaged in each activity for each individual scan (N=889). I used Spearman rank correlations to test the relationship between (i) the proportion of immature individuals and (ii) the proportion of mature individuals engaging each activity for each scan, using all 20 behavioural categories. I used a Wilcoxon signed rank test to test for differences in the proportion of immature and mature individuals engaging in each activity in each scan.

Behavioural Synchrony and the Kappa Coefficient of Agreement

I chose the Kappa coefficient as the measure of behavioural synchrony, based on Asher & Collins' (2012) conclusion that Kappa represents the best measure of behavioural synchrony. Kappa was designed as a measure of agreement between raters (Cohen 1960, Fleiss 1971, Siegel and Castellan 1988). It measures the extent of observed behavioural synchrony in a group and determines whether the observed value is significantly different to chance.

Kappa (*K*) is calculated as

$$K = \frac{P(A) - P(E)}{1 - P(E)}$$

where *P(A)* is the observed proportion and *P(E)* is the expected proportion of synchrony. *K* can range from -1 to 1, with *K* = 1 indicating complete synchrony, *K* = 0 indicating that observed synchrony was no different than expected by chance, and *K* = -1 indicating asynchrony. Table 4.3 shows two attempts to formalise the strength of agreement based on the magnitude of Kappa, which while arbitrary and not universally accepted (Gwet 2012), allow for some interpretation of Kappa in a wider context.

Table 4.3: Two guidelines for the interpretation of the magnitude of Kappa; A) Landis, J.R.; Koch, G.G. (1977). "The measurement of observer agreement for categorical data". *Biometrics* 33 (1): 159–174.; B) Fleiss, J.L. (1981). *Statistical methods for rates and proportions* (2nd ed.). New York: John Wiley

A		B	
Kappa	**Strength of Agreement**	**Kappa**	**Strength of Agreement**
<0.00	Poor		
0.00-0.20	Slight		
0.21-0.40	Fair	<0.40	Poor
0.41-0.60	Moderate	>0.40 < 0.75	Fair to Good
0.61-0.80	Substantial	>0.75	Excellent
0.81-1.00	Almost Perfect		

The observed proportion of synchrony, *P(A)* is calculated using the number of pairs of animals engaged in the same behaviour:

$$P(A) = \frac{1}{N}\sum_{i=1}^{N} Si$$

where *Si* is the proportion of the number of pairs of animals engaged in the same behaviour in the *i*th observation of a total of *N* observations.

The expected proportion of synchrony *P(E)* is calculated by assessing the number of pairs of animals that would be engaged in the same behaviour by chance based on the frequencies of behaviour states:

$$P(E) = \sum_{j=1}^{m} cj/Nk$$

where c is the total number of observations for the *j*th behaviour of a total of *m* behavioural categories, and *k* is the group size. Here, *cj/Nk* can be simplified to *Pj*, which is the proportion of behaviours seen in the *j*th category.

The significance of K (i.e., H_0: K=0, H_1:K>0 or K<0) is calculated using the variance of *K*, *var(K)*:

$$var(K) = \frac{2}{Nk(k-1)} \frac{P(A) - (2k-3)[P(A)]^2 + 2(k-2)\sum p_j^3}{[1-[P(A)]^2}$$

Using *var(K)* it is possible to calculate a *z* value as:

$$z = \frac{K}{\sqrt{var(K)}}$$

This z value can be compared against a standard probability distribution table to establish whether it exceeds the α = 0.01 where *z* = 2.32.

I used a custom PERL script (Foerder et al 2013, Chodorow *personal communication*), to calculate K for 18 different data treatments (6 levels of behavioural categorisation for each of the whole group, immature-only group, and mature-only group). As the sample size was the same as the number of treatments, and because the data are not independent (i.e. both the mature group and the immature group are present in the whole group calculations), inferential statistics are not possible with this sample.

Instead, I report the statistical significance of the synchrony measures themselves, along with a visual description of the major features of the derived Kappa values.

Randomization

To test the effects of group composition on behavioural synchrony, I assigned each individual in each scan randomly to either an immature or mature subset using the total number of individuals in each scan and maintaining the behaviour of each individual, while maintaining the observed number of each group in each scan (Foerder et al 2013). I generated Kappa values for each randomization for both immature and mature subsets. I then compared the distributions of Kappa produced by these randomised data to the observed values of the unmixed subsets. I ran 1000 permutations for each of the treatments, with 6 tests for matures and 6 tests for immatures (2/5/10 behaviours X height included/height not included). I chose a threshold of 1000 permutations as this corresponds to $P<0.001$ if the observed values fall outside any of the randomized values.

4.3. Results

4.3.1 – Prevalence of Activities in Immature and Mature Animals

Locomotion was the most prevalent activity for all groups, with feeding on subterannean items and travel feeding being the next most prevalent (Figure 4.1). Several behavioural categories were rarely observed, particularly activites taking place above the ground as a result of the generally terrestrial nature of this study population.

The behaviour of immature and mature individuals was significantly correlated in all but one of the behavioural categories (feeding on grasses at a height above the ground) (Table 4.5). The strength of the significant associations varied from 0.15 for resting in cover on the ground, to 0.723 for feeding on subterranean food items on the ground.

I found significant differences between the proportion of time spent by immature and mature individuals in 10 of the 20 behavioural activities (Table 4.4), with 6 of these relating to activities on the ground and the remaining 4 to activities above the ground. I found significant differences at both the ground and above the ground for the

proportion of time engaged in social activities and the proportion of time spent moving Table 4.4).

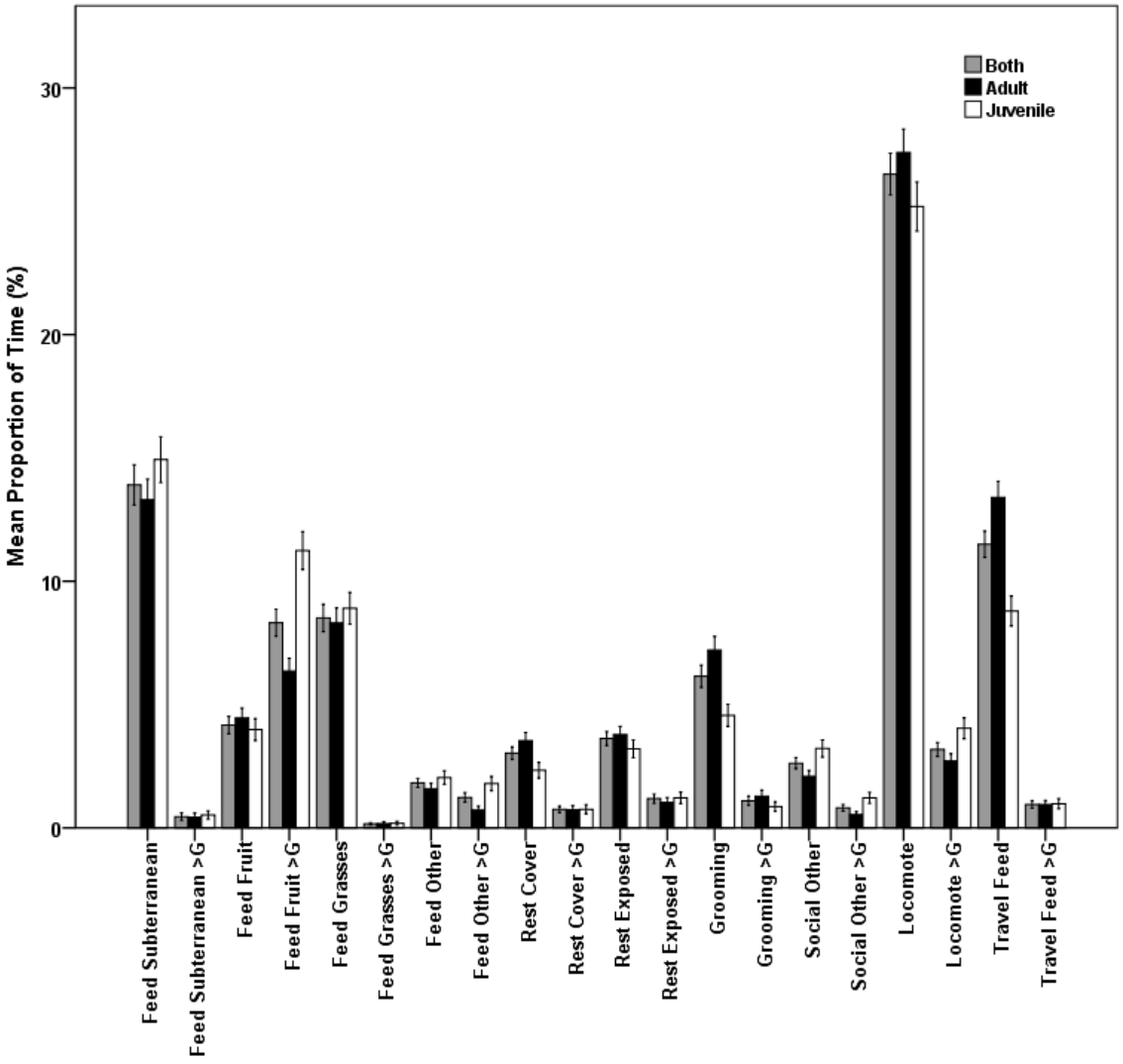

Figure 4.1. Mean +- SE proportion of time spent engaging in each of 20 behavioural categories by all individuals, mature animals only and immature animals only. Entries marked ">G" indicate the behaviour occurred above the ground.

Table 4.4. Results of Spearman correlation tests and Wilcoxon signed-rank tests comparing the proportion of individuals engaging in each of 20 behavioural categories by mature and immature animals in each scan (N=889). Height 0 indicates the behaviour took place on the ground, >0 indicates the behaviour took place above the ground. Significant correlations and pairwise differences are in bold.

Number of Behaviours				Spearman		Wilcoxon Signed-rank	
10	5	2	Height	Rho	P	Z	P
Feed Subterranean	**Feed**	**Inactive**	0	**0.723**	**<0.001**	**-2.228**	**0.026**
			>0	**0.518**	**<0.001**	-0.663	0.507
Feed Fruit			0	**0.472**	**<0.001**	-1.268	0.205
			>0	**0.584**	**<0.001**	**-7.647**	**<0.001**
Feed Grasses			0	**0.537**	**<0.001**	-1.290	0.197
			>0	-0.008	0.813	-0.189	0.850
Feed Other			0	**0.163**	**<0.001**	-0.1727	0.084
			>0	**0.295**	**<0.001**	**-3.851**	**<0.001**
Rest Covered	**Rest**		0	**0.15**	**<0.001**	**-3.024**	**0.002**
			>0	**0.244**	**<0.001**	-0.122	0.903
Rest Exposed			0	**0.347**	**<0.001**	-1.922	0.055
			>0	**0.306**	**<0.001**	-0.478	0.633
Social Grooming	**Social**		0	**0.559**	**<0.001**	**-5.814**	**<0.001**
			>0	**0.47**	**<0.001**	-1.766	0.077
Social Other			0	**0.347**	**<0.001**	**-2.929**	**0.003**
			>0	**0.418**	**<0.001**	**-3.177**	**0.001**
Move	**Move**	**Active**	0	**0.504**	**<0.001**	**-2.444**	**0.015**
			>0	**0.35**	**<0.001**	**-3.152**	**0.002**
Travel Feed	**Travel Feed**		0	**0.334**	**<0.001**	**-6.751**	**<0.001**
			>0	**0.248**	**<0.001**	-0.422	0.673

4.3.2 – Behavioural synchrony of different treatments

The observed (PA) and expected (PE) values of synchrony decline with the number of behaviours in the analysis (Figure 4.2), but there is little difference in Kappa between the different levels of behavioural categorisation or groups (mean 0.2525 +- 0.0171 (SE), range 0.2273 in the whole group, 5 behaviour condition to 0.2884 in the immature only, 2 behaviours including height condition). However, the *var(K)* values generated for these tests were very small (0.00001 – 0.00020), with derived Z values far exceeding the threshold of 2.32 (range 18.13-78.34, Table 4.5) indicating that for all treatments

behavioural synchrony was significantly higher than would be expected than chance alone. For each of the different number of behavioural categories, Z-scores are highest for a group containing all group members, next highest for the mature-only subset, and lowest for the immature-only subset.

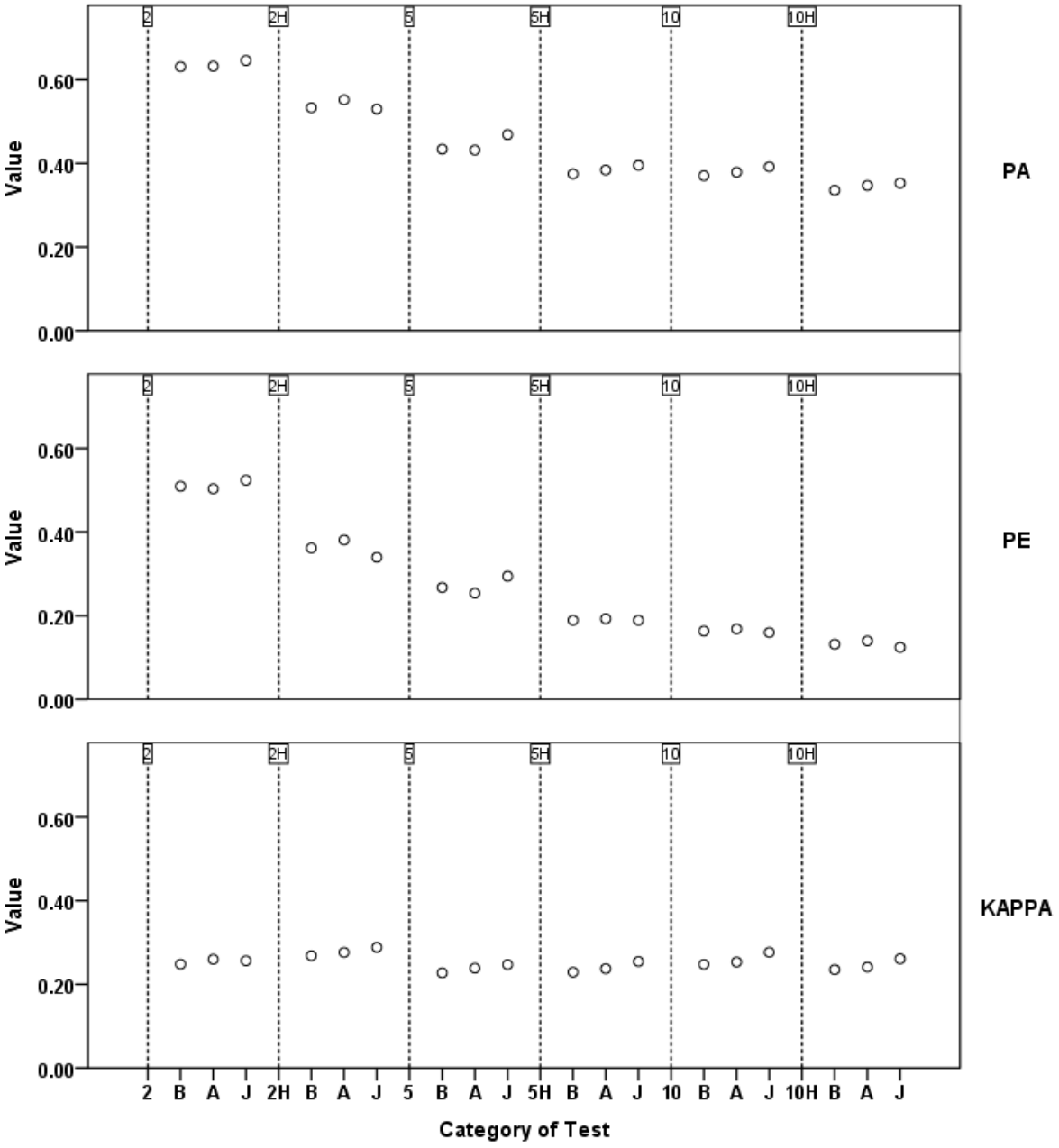

Figure 4.2. PA, PE and Kappa values for 18 tests. B = All individuals, A = Mature individuals only, J = Immature individuals only. The dotted line shows the number of behaviours used in the test, with H indicating that height above ground was included (e.g., 2 = 2 behaviours, 5H = 5 behaviours including height above the ground

Table 4.5: var(K) and associated Z-scores for the Kappa coefficients for each number of behaviours and group composition.

Number of behaviours	Whole group		Mature		Immature	
	var(K)	Z	var(K)	Z	var(K)	Z
2	0.00003	45.30	0.00007	31.03	0.00020	18.13
2 + Height	0.00002	60.04	0.00006	35.67	0.00010	28.84
5	0.00002	50.81	0.00003	43.55	0.00009	26.06
5+ Height	0.00001	72.47	0.00002	53.06	0.00005	36.01
10	0.00001	78.34	0.00002	56.66	0.00004	43.73
10+ Height	0.00001	74.32	0.00002	53.91	0.00003	47.64

Because of the low variation between the Kappa scores for the different treatments and need to display PA, PE and Kappa on the same graph at the same scale (Figure 4.2), I have presented the Kappa values at a more detailed level (Figure 4.3) to better show the differences between the treatments.

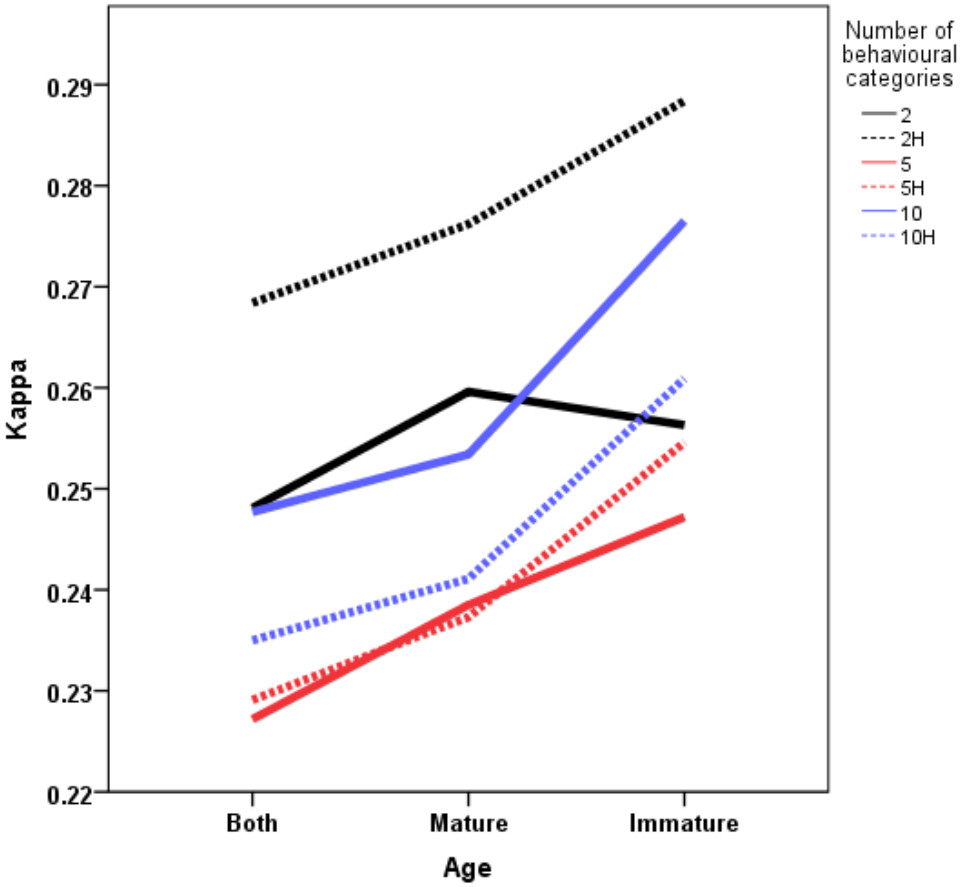

Figure 4.3. Kappa values by age class for each test. Note that the Y-axis does not begin at the origin. H indicates that height above ground was included in calculating Kappa.

4.3.3. Random assignment of individuals to groups

Randomly assigning individuals to the mature subset reduced behavioural synchrony. All six randomization tests for incorporating immature individuals into the mature subset were significantly less synchronised than subsets containing only mature individuals (Figure 4.4). In five of these conditions, the observed value for Kappa was higher than any randomised subset ($P<0.001$), with the exception being the two behaviour including height condition in which a single randomised group was more synchronised ($P=0.002$). Randomly assigning individuals to the immature subset, however, had no significant impact on behavioural synchrony in any treatment (range $p=0.065$ to $p=0.383$, Fig 4.4).

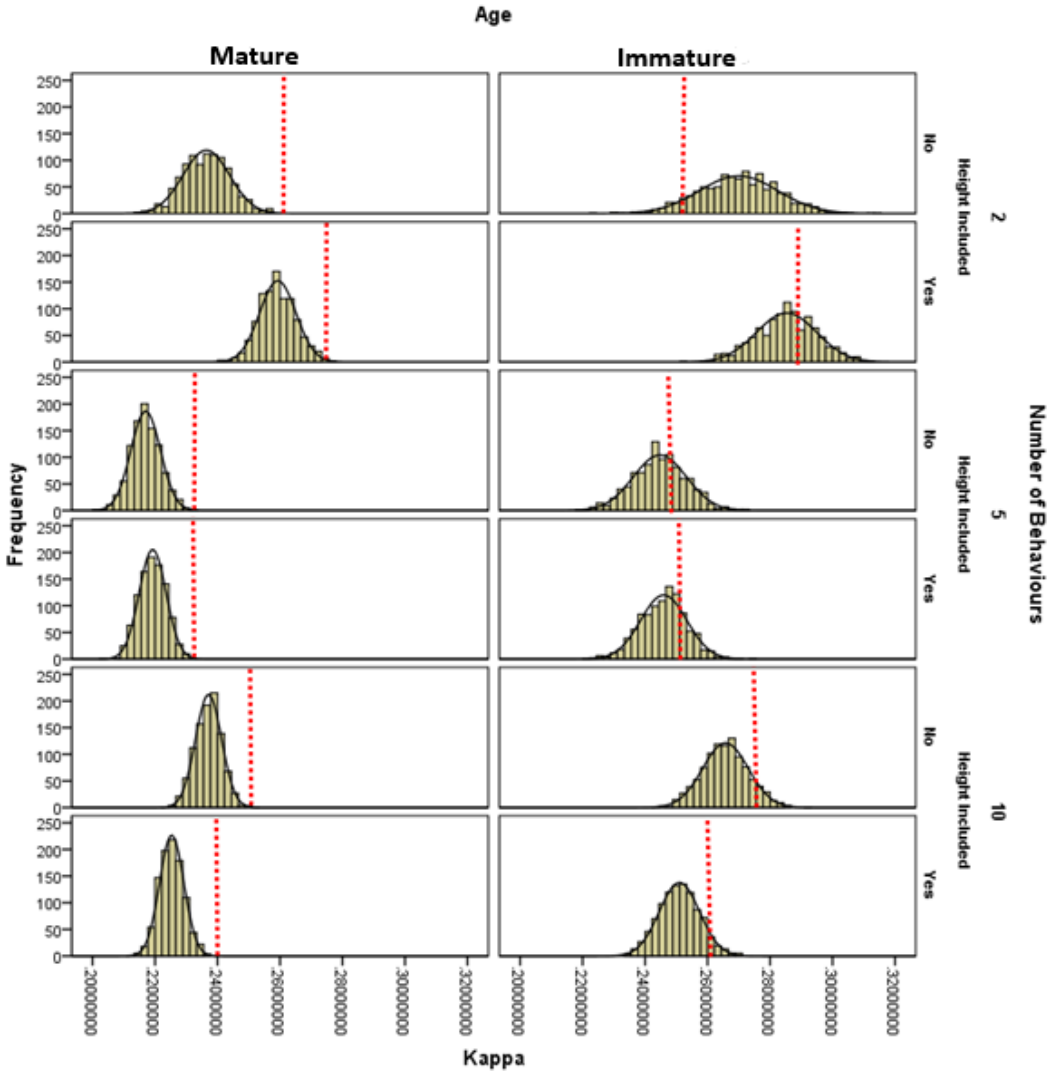

Figure 4.4. Histogram and distribution of Kappa values for 1000 randomization tests for the 6 different behavioural categories. The red dotted line indicates the Kappa value for the observed data

4.4. Discussion

In this chapter I assess the extent to which the behaviour of immature and mature chacma baboons differs, and the effect that this has on behavioural synchrony. I also address the extent to which the number of behaviour categories and the addition of height above ground has an impact on measures of behavioural synchrony. While some of my predictions are supported by the data, other findings conflict with both my predictions and the literature.

My first prediction, that the behaviours of immature and mature individuals in a scan will be correlated but that they will also differ, received some support. All but one behaviour showed significant correlations between the behaviour of immature and mature baboons, although many of these correlations were weak. However, I also found significant pair-wise differences between immatures and matures in half of the behavioural categories. The behaviours of adults and juveniles appears to be relatively coordinated in terms of the proportion of individuals in each class engaging in the same activity. However, many of these categories take up a marginal amount of time, and are characterised by a high proportion of zero values.

My prediction that behavioural synchrony will be highest in groups composed of individuals of similar ages, and lowest in groups that include all individuals is strongly supported by the data. Kappa values for the immature subset were higher than both the mature subset and the combined group across all data treatments with the exception of the binary active/inactive treatment in which the mature subset showed higher synchrony. The mature group was also more synchronised than the combined group for all treatments. The observed Kappa values for all treatments indicated low levels of behavioural synchrony, with even the highest value of 0.288 suggesting only a ‘fair’ magnitude of synchrony (Gwet 2012). The synchrony was significantly higher than expected by chance. Given a large enough sample any Kappa value greater than zero will be statistically significant (Viera & Garrett 2005), and Rook and Penning (1991) advise caution on the interpretation of the significance of Z-scores in the case of large samples as presented here. Nevertheless, these findings support the prediction that

individuals that are more similar in size will have higher levels of behavioural synchrony with one another (Ruckstuhl 1999, Aiwaz & Ruckstuhl 2011, Foerder et al 2013).

Given the low Kappa values found in my study across all treatments, it is likely that behavioural synchrony is not a major factor in baboon societies, and that groups can maintain cohesion and coordinate despite engaging in different activities at the same time. In contrast to other dimorphic species in which the scheduling of activities between the sexes requires sexual segregation (e.g. ungulates Ruckstuhl 1998, Michelena et al 2006), chacma baboon groups comprise permanent associations of adult males and females and their dependent offspring. Given the general differences in activity budgets found in this study population (Chapter 3), baboon groups may be resilient against the effect of individuals engaging in different activities at the same time. Contact calls (Cheney et al 1996, Rendall et al 2000, Ey & Fischer 2011), move grunts (Owren et al 1997, Rendall et al 1999, Meise et al 2011), and general visual monitoring of other group members (Alberts 1994, McNelis & Boatright-Horowitz 1998) may allow baboons to prioritise their own diverse behavioural needs, while still maintaining group cohesion. As such, the long juvenile period in baboons may be facilitated by the low levels of group-level synchrony, by potentially reducing competition for food with adult conspecifics, while also allowing for them to engage in their own specific behaviours (i.e. play) without becoming separated from the rest of the group.

I also predicted that behavioural synchrony would decrease as the number of behavioural categories increased. The results provided mixed support for this prediction. In contrast to previous research that showed that behavioural synchrony decreases as the number of behavioural categories increases (Asher & Collins 2012), I found that while Kappa values were generally highest in tests with the lowest amount of behavioural categories, they were not lowest in tests with the highest number of categories. Behavioural synchrony was lower in both of the 5 behaviour treatments than in the 2 behaviour or 10 behaviour conditions, while in an immature-only subset, behavioural synchrony was higher in the 10 behaviour condition than in one of the 2 behaviour treatments. The relationship between behavioural synchrony and the number of behavioural categories is therefore not as straightforward as expected (e.g. Asher & Collins 2012). While the range of Kappa values was low across the different data

treatments, both the observed values (PA) and expected values (PE) decreased with the number of behavioural categories incorporated. Kappa is derived directly from these two values, and effectively regulates the effect of increasing the number of categories, meaning it should allow for comparisons between studies, even under different observational conditions and levels of behavioural categorisation.

The results also provided mixed support for the prediction that the inclusion of height above ground would decrease behavioural synchrony. While in some situations it led to a decrease in behavioural synchrony, in others it led to an increase, most markedly in the two behaviour category condition. While including whether an individual was on or above the ground effectively doubles the number of behavioural categories, time spent above the ground was low for all classes relative to time spent on the ground, and this population was primarily terrestrial (Chapter 3). Given the inconsistency in this effect, height above ground warrants further investigation in studies of behavioural synchrony in non-human primates. The vertical space is an important dimension in many species (Kimura 2002), and age-sex classes differ in their use of vertical space (Menard 1985). Although I was unable to determine whether the differences between conditions are statistically significant, these differences merit further exploration.

My final prediction that randomly assigning individuals to either the immature or mature group would decrease behavioural synchrony also found limited support. In the mature subset, the observed Kappa values were universally higher than the randomised values, while in the immature subset, the observed Kappa values were not significantly different to those produced through random assignment. This indicates that for mature individuals, the presence of immatures decreases group synchrony, while the behavioural synchrony of immature individuals is less affected by the inclusion of mature individuals. This finding is somewhat surprising given the fact that animals that are more similar in size are expected to be more synchronised (Ruckstuhl 1999, Aiwaz & Ruckstuhl 2011, Foerder et al 2013). This suggests that the random assignment of individuals to the mature or immature groups should lead to decreased levels of synchrony in both groups, not just in the mature group. Additional research on primates groups of differing sizes and demographic profiles may shed further light on this question.

This study built on previous theoretical and practical studies on behavioural synchrony, particularly the general utility of the Kappa coefficient as a means of determining behavioural synchrony at multiple levels of analysis. The results of this study suggest that it should be possible to develop a robust behavioural synchrony measure that can be compared across studies regardless of the number of categories used in data collection and analysis. Kappa represents a potentially very useful source of information for further analysis of existing data.

4.5. Conclusions

This is the first study to apply the Kappa coefficient to behavioural synchrony in primate groups. I conclude that individuals that are more similar in age exhibit higher levels of behavioural synchrony, and that the demographic composition of a group will affect synchrony. However, the extent of such synchrony is low across all treatments, suggesting that behavioural synchrony is not an important factor in baboon societies. Individuals in chacma baboon groups engage in different activities at the same time, while still remaining a cohesive group. While measures of behavioural synchrony are affected by the number and type of behavioural categories used, this study highlights that this relationship is not a simple one.

5 The Effects of Age, Sex and Social Dominance on Individual Movement Patterns

5.1 Introduction

Movement, defined as the process by which individual organisms are displaced over time (Louriero et al 2007, Nathan et al 2008), is ubiquitous among animal populations. The requirements of individuals to acquire diverse resources such as food, shelter and breeding partners, which may themselves be mobile, sparsely distributed or ephemeral, can lead to complex movement patterns. Central to this is animal motility; animals are able to move spontaneously through their habitats. Movement comes at an energetic cost (Taylor et al 1970, Taylor 1980, Leonard & Robinson 1997), and mammals are adapted to maximise the gains and minimise the costs of foraging and travel (Pontzer & Kamilar 2009).

The emerging field of movement ecology proposes four paradigms for investigating animal movement: optimality, biomechanical, cognitive and random approaches (Nathan 2008, Nathan et al 2008). Optimality refers to optimal foraging theory (MacArthur & Pianka 1966, Pyke et al 1977, Stephens & Krebs 1986), which has been proposed as a useful means of explaining the adaptation of animals to the resources available and how they forage for them, yet has been criticised largely on the basis that 'optimization' is an inappropriate concept with regards to animal behaviour (Pierce & Ollason 1987, Perry & Pianka 1997). The biomechanical approach centres on issues relating to the actual physical mechanisms of movement in organisms, energetics and the capacity for movement (e.g. Vogel 2003, Steudel-Numbers 2003). The cognitive approach centres on the decision-making processes and navigation (Sutherland & Hamilton 2004, Janson & Byrne 2007). The random approach is characterised by descriptions of movement paths and statistical models derived from theoretical concepts, such as the random walk and diffusion, often characterised as Levy flights and Brownian motion, respectively (Bartumeus & Levin 2008, Benhamou 2007, Smouse et al 2010).

Studies of animal movement patterns can be broadly split into two main categories: those which seek to examine the ranging patterns of populations or individuals via home range analysis (Seaman & Powell 1996, Getz & Wilmers 2004) and those which seek to examine the path structure of animal movement (Nams 2005, Noser & Byrne 2007). Of the latter, a key component of analysis is the tortuosity of the path that an animal takes through the landscape (Benhamou 2007). Path tortuosity is the degree of convolution or straightness of a path (Bascompte & Villa 1997, Louiero et al 2007), and is related to the efficiency of movement whereby the closer a path between a starting point and a goal is to a straight-line segment, the more efficient the path (Benhamou 2004).

Several indices of tortuosity have been developed, ranging from a simple straightness index (Batschelet 1981), characterised as the ratio of the straight line distance between two points and the actual path taken between these points, to complex sinuosity estimates (Bovet and Benhamou 1988, Benhamou 2004), which rely on knowledge of turning angles and step lengths along a path. Importantly, the different indices proposed do not measure the same thing, differ conceptually and theoretically, and are affected differently by the scales of measurement used (Almeida et al 2010). For example, sinuosity is a specific type of tortuosity resulting in a correlated random walk, while the straightness index is more appropriately a measure of ballistic movements oriented towards a distant goal (ibid.).

One commonly used measure of tortuosity is the fractal dimension (*D*) of a path. Based on the concept of fractals (Mandelbrot 1977, 1983), the fractal dimension was first proposed as a means of analysing the complexity of growth paths of cells (Katz & George 1985), and independently proposed as a means of analysing animal movement paths (Dicke & Burrough 1988). While the use of fractal dimensions in the context of animal movement is not without its critics (Turchin 1996, Benhamou 2004), much of this criticism relates to the extent to which the fractal dimension is scale-independent and self-similar. Self-similarity, whereby an object exhibits a repeating pattern in which a portion of the object will exhibit the same properties of the entire object, is a fundamental concept of fractals (Mandelbrot 1983). In the context of movement paths, this means that any given portion of a travel route should reflect the pattern of the entire travel route, yet to date such scale-independent patterns relating to 'true' or

'ideal' fractals are contested in animal movement patterns (Turchin 1996, Benhamou 2004), and indeed for ecological data in general (Halley et al 2004). However, even if movement paths are not strictly fractal in nature, fractals can still be usefully applied to natural phenomena as a measure of complexity (Nams & Burgeois 2004, Almeida et al 2010).

The fractal dimension can be used to approximate the tortuosity of a travel route via its space-filling properties (Katz and George 1985, Bascompte & Villa 1997, Tremblay et al 2007). Additionally, as the log of the fractal dimension follows a normal distribution, it is suitable for parametric testing, allowing analysis of the tortuosity of travel routes with respect to biotic and abiotic factors. Fractal dimensions have been used in a range of contexts and a variety of species (e.g. seasonal variation in travel in Iberian wolves (*Canis lupes*), Bascompte & Villa 1997; movement related to known food sources in reindeer (*Rangifer tarandus*), Marell et al 2002; path tortuosity in relation to patchy habitats in red-backed voles (*Myodes* spp.) and deer mice (*Peromyscus* spp.), Nams 2005; movement patterns related to resources and individuals differences in Eurasian badgers (*Meles meles*), Louriero et al 2007). Several studies using the fractal dimension have examined age and sex related differences in tortuosity. For example, females with young offspring show more restricted, and therefore more tortuous, travel routes compared to females without young in both female wolves (*Canis lupes*) and white-tailed deer (*Odeocoileus virgianus*, Bascompte & Villa 1997, Webb et al 2009). While no significant age and sex differences were found in the path tortuosity of Eurasian badgers, tortuosity was related to the presence of dens and latrines throughout in the landscape (Louriero et al 2007).

Investigations into animal movement patterns have often been constrained by the data collection methods available. For small animals, a common method has been the attachment of spools of thread to individual animals and then recording the travel route via the thread pattern as it catches on vegetation (Nams 2005), while for insects in a controlled environment it is possible to simply trace travel paths by placing the animal on a surface and tracing their route with a pen (Angilletta Jr et al 2008). For large animals, radio-tracking is often the best or only solution (Harris et al 1990), and while GPS collars and tags are widely available, they are hindered by expense and battery-life

and subject to technical malfunctions (Kaczensky et al 2010). Both of these methods also involve a large investment in terms of capture and tagging of subjects, collecting fixes via radio-telemetry, and retrieval of data loggers in the case of GPS equipment. Studies of animal movement are therefore often characterised by a small sample size, with data often recorded with relatively large timespans between locational fixes.

Studies of primate movement have often relied on data from either GPS collared individuals (e.g., Ren et al 2008, Pebsworth et al 2012, Strandburg-Peshkin et al 2015) or from waypoints taken at the central mass of the group (e.g. Willems & Hill 2009, Ansensio 2011, de Raad 2012). This is useful for home range estimations and studies of resource use, but does not reveal individual differences in movement. A recent investigation of ranging patterns in baboons successfully collared ~80% of adult and sub-adult members of a single group, with spatial data recorded at one fix per second (Strandburg-Peskin et al 2015). However, such fine detail mean that collars can only record data for between 14-30 days, while data storage constraints require the downloading of data daily. Remotely sensed information therefore represents a trade-off between fidelity and detail of information versus longevity.

Habituated primate groups present a potential source of great insight into animal movement, largely because they can be followed closely by observers. By following focal animals with a GPS unit attached to the observer it is possible to obtain spatial data including travel routes for multiple individual subjects (Valero & Byrne 2007, Lodge 2012) without the need for estimation of animal movements (e.g. Isbell et al 1999) or intrusive tagging. Spatial data can be collected in tandem with behavioural data on the focal animal as opposed to inferring social dynamics and interactions through the GPS data collected (e.g. Strandburg-Peshkin 2015). Such an approach allows for detailed multi-level analysis of the relationships between animal movement patterns and animal behaviour, particularly the social impact of group-living on individuals' movement.

Most primates live in groups, and, with the exception of fission-fusion societies, travel together as a group (Bates & Byrne 2009). As such, studies on primate movement patterns have tended to focus on group movements rather than on individual variation (ibid). Being part of a group leads to the potential for intra-group competition, and larger

groups require further distance to be travelled by individuals in order to obtain resources as a consequence of food patch depletion and increased avoidance of other foraging animals (Chapman & Chapman 2000, Gilespie & Chapman 2001). The travel costs imposed by group living is not equivalent across all group members, and dominance rank may constrain the movement of individuals within a group. For example, lower-ranked females travel longer and more tortuous routes than do higher-ranked females (e.g. patas monkeys (*Erythrocebus patas*) and vervets (*Chlorocebus pygerythrus*) Isbell et al 1999b, rhesus macaques (*Macaca mulatta*) Beisner and Isbell 2009). Rather than the indirect effect of dominance rank itself, it may however be the direct consequences of agonism that may be better indicators for fitness (Wheeler et al 2013). Rates of agonism in female primates have been found to be more positively associated with group size and the extent of terrestriality than the availability of resources (*ibid*). It is important to study the potential effects of agonism on other age and sex classes to determine whether such constraints apply to all group members

Primates live in a complex social world, and the behaviour of group members is dependent on their social surroundings as well as on individual characteristics, priorities and motivations. Activity patterns differ among age and sex classes (chapter 3), with group members exhibiting low levels of behavioural synchrony, particularly between immature and mature individuals (chapter 4). However, they move through the landscape relatively cohesively, from morning sleeping site to evening sleeping site. As different animals cannot occupy the same space at the same time, compromises will need to be made that reflect individual differences in activity and in their abilities to exert dominance on others as animals move together. Given the behavioural differences between the age-sex classes, it is important to examine whether or not these differences in general activity patterns are also expressed in how animals move through the physical landscape, and whether these movements are mediated by the social landscape.

Aims and Objectives

In this chapter I examine the effects of age, sex and the frequency of agonism given and received on individual movement patterns. I have chosen to focus on these variables as they may reflect individual differences in movement behaviour, whereas environmental

or seasonal factors may simply reflect group level differences in movement over time. Such environmental parameters will however be used as control variables in analyses. I use field observations of chacma baboons to examine three key movement parameters: the total distance travelled, the straightness index and the fractal dimension. I test three predictions:

1) Adult individuals will exhibit less tortuous movement paths than immature individuals due to their greater knowledge and experience of the landscape, and their greater capability in acquiring resources.

2) There will be sex differences in path tortuosity and the distance travelled by males and females as a consequence of their differing behavioural priorities and general activity patterns (Chapter 3).

3) Path tortuosity will increase with the amount of agonism received but not with the amount of agonism given, and individuals who receive more agonism will also travel further distances. Individuals that receive more agonism are more likely to travel further and search farther afield for resources.

5.2 Methods

5.2.1 Study site

I collected data over 19 months (November 2011 - June 2013) at Lajuma Research Centre in the Soutpansberg mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). Further details on the study site are in the Methods chapter.

5.2.2 Subjects

The subjects of data collection were a group of baboons known as House Troop. Group size fluctuated during the study period from approximately 74 to 80 individuals as a result of births, migration and mortality. Full details of group demographics are in the Methods chapter.

5.2.3 Data Collection

I conducted 15 minute focal samples on selected individuals, recording the activity of the focal subject and the social interactions that the subject was involved in. See Methods for full details of the data collection protocol.

I recorded spatial information in UTM format using a Garmin C62s GPS set to record coordinates at 10 m intervals during all contact with the group. I used a distance rather than a time-recording protocol to ensure that step-lengths would be evenly spaced spatially, and chose 10 m intervals based on the margin of telemetric error due to the topography (±3-5 m). A shorter step-length would be more prone to inaccuracies, while a longer step-length would decrease the precision of recording. I attempted to maintain a constant distance of approximately 5 m from the focal animal, and to follow the exact path the animal took. Where this was not possible due to inaccessibility of the terrain or vegetation, I took the best approximate straight path. I recorded a waypoint at the beginning and at the end of each 15 minute focal sample, allowing me to match the GPS data to the behaviour of the focal animal and to ensure that only movement made during each focal sample was used in analysis.

Due to potential inaccuracy in the collection of telemetry data in a complex environment, I selected only focal samples which had >60 seconds of recorded movement (either locomotion or foraging). The final data set included 1128 focal samples collected on 50 different individuals of mixed age and sex classes (Table 5.1). 14 individuals are represented in two age classes, as they matured during the study (one young juvenile to older juvenile; two older juvenile males to pubescents; two older juvenile females to adolescents, three pubescent males to adolescents, six adolescents to adults).

Table 5.1: Sample size for analysis by age and sex including the number of subjects, the number of focal samples, and the mean number of focal samples per individual

Age	Female			Male		
	N. Individuals	N. Focals	Mean N. focal samples +- (SD)	N. Individuals	N. Focals	Mean N. focal samples +- (SD)
Young Juvenile	2	30	15 (18.38)	1	15	15 (0)
Old Juvenile	3	33	11 (13.23)	9	314	34.89
Pubescent	N/A	N/A	N/A	5	79	15.8 (7.60)
Adolescent	7	198	28.29 (12.52)	8	98	12.25
Adult	18	209	11.61 (9.07)	10	152	15.2 (18.78)

5.2.4 Data Processing

Dependent Variables

I used the GPS data to calculate three dependent variables for analysis: the distance travelled during a 15 minute focal sample, the straightness index (*SI*), and the fractal dimension (*D*) of the travel path. I derived these values from the following data:

i) *Total Distance Travelled (L):* the total distance travelled during the focal following the movement path of the focal individual.

ii) *Straight-Line Distance Travelled (SL):* the straight-line path (displacement) between the start and end waypoint of each focal.

iii) *Number of Steps (n):* the number of GPS data points collected for each focal. Given the standardised step-length of 10 m, a travel route of 50 m would have ~5 steps, while a 500 m route would have ~50 steps.

Iii) *Planar Diameter (d):* the maximum distance between any two coordinates in a focal sample. As the GPS data were collected in UTM grid format, the distance between two points can be calculated using $c = \sqrt{a^2 + b^2}$ where *a* = the horizontal displacement between two points, *b* = the vertical displacement between two points, and *c* = the total displacement between two points (the hypotenuse).

The distance travelled is simply *L*, while the straightness index and fractal dimension were calculated as

$$\textbf{\textit{Straightness Index}} = \frac{SL}{L}$$

$$\textbf{\textit{Fractal Dimension}} = \frac{log(n)}{log(n)+log(d/L)}$$

The straightness index is a value from 0 to 1 measuring how straight a travel path is relative to the final position (Batschelet 1981). A value of 1 indicates the most direct and efficient straight-line route, while a value close to 0 indicates an inefficient and tortuous path with little displacement between the start and end points relative to the actual distance travelled.

The fractal dimension represents how much space on a curvilinear plane is filled by a path (Katz & George 1985), with the minimum value of 1 indicating a straight-line (i.e 1-dimensional). Increasing values suggest more convoluted paths as the movement fills more of the plane with a value of 2 indicating a 'full' plane (i.e., 2-dimensional). While fractal dimensions should fall between values of 1 and 2, values up to a theoretical infinite maximum are possible if a travel route repeatedly crosses over itself, indicative of a restrictive or constrained travel route.

Figures 5.1 and 5.2 show examples of four randomly selected travel routes, with the values used to calculate the dependent variables. The values are in Table 5.2.

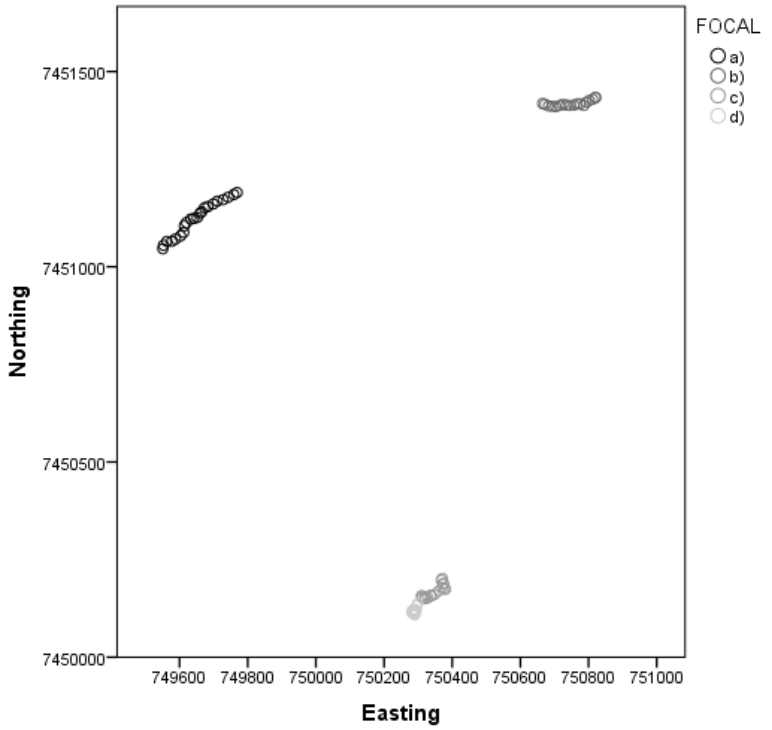

Figure 5.1: Four randomly selected focal tracks illustrating variation in the scale of movement in a 15 minute period. a) Older juvenile male; b) Adult Female; c) Adult Male; d) Older juvenile Male. Axes represent coordinate values in UTM 35K

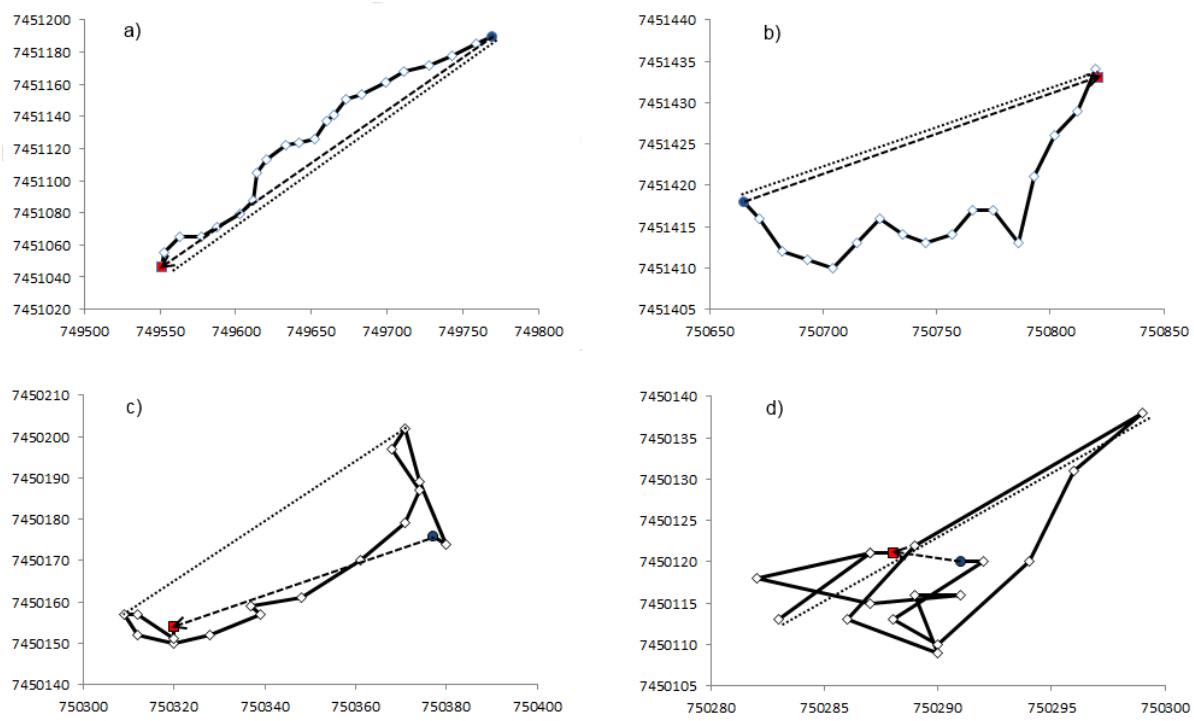

Figure 5.2: Examples of 4 routes taken by focal animals a,b,c,and d. Start of route = blue circles; End of route = red squares; Total distance travelled (*L*) = solid black line; Number of steps (*n*) = clear diamonds; Straight-line distance (*SL*) = dashed line with arrow; Planar diameter (*d*) = dotted line. Axes represent coordinate values in UTM 35K at different scales; see figure 5.1 for relative position and size of routes.

Table 5.2: Calculated values of the Straightness Index (SI) and Fractal Dimension (D) for the 4 routes displayed in Figures 5.1 and 5.2. n= number of steps along the path; L = total distance travelled by the subject (m); SL = straight-line distance of travel; d= planar diameter of travel

ID	Age Class	Sex	Month	Year	*n*	*L*	*SL*	*d*	*SI*	*D*
a)	Juv 2	Male	Sep	2012	21	269	261	261.2661	0.97026	1.009674
b)	Adult	Female	Jul	2012	17	166	157	156.7195	0.940241	1.012191
c)	Adult	Male	Dec	2012	18	148	62	77.33693	0.418919	1.289578
d)	Juv 2	Male	Feb	2013	18	118	3	30.36445	0.025424	1.885484

Values of the straightness index and the fractal dimension were almost perfectly correlated (Spearman's Rho = -0.932, $p<0.001$; Figure 5.3). I therefore focus on the fractal dimension as the key measure of tortuosity rather than examining both measures. A previous comparison between five measures of tortuosity found that the straightness index was more prone for bias produced by both sample size and location errors relative to the more robust fractal dimension (Almeida et al 2010). While the fractal dimension used in Almeida et al's study was derived from the Fractal D index (Nams 2005) rather than the measure I implemented in this study (Katz & George 1985), it is likely that the generally robust nature of the fractal dimension will be the same.

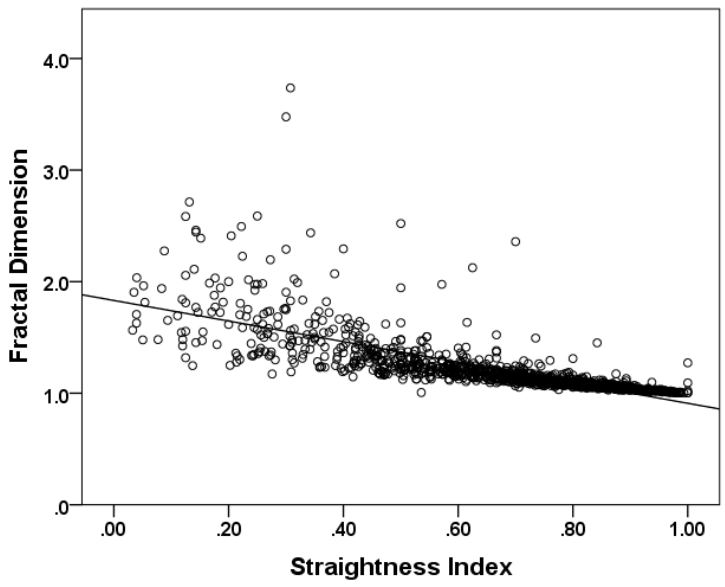

Figure 5.3: Correlation between the straightness index (SI) and the fractal dimension (D) of each travel path. N= 1128.

Independent variables

I derived age and sex from the physical characteristics of the focal animal (see Methods chapter). To measure agonism given and received, I used counts of events during each focal sample (see Methods for ethogram). Both agonism received during a focal (mean = 0.59 +- 0.98, minimum = 0, maximum = 7) and agonism given (mean = 0.55 +- 0.99, minimum = 0, maximum = 8) were characterised by the absence of agonism in the majority of focals (no agonism received by the focal subject in 717/1128 = 63.6% of focals; no agonism given by the focal subject in 757/1128 = 67.1% of focals).

5.2.5 Analysis

I used Generalised Linear Mixed Models (GLMMs) using the GENLINMIXED function in SPSS 22.0 for each dependent variable to examine the effects of age, sex (and their interaction) and the number of agonistic behaviours received and given during each focal sample. I included season (Summer 1, January-March 2012; Winter 1, April-September 2012; Summer 2, October 2012-March 2013; Winter 2, April-June 2013) and time of day (4 time blocks, 06:00-09:00, 09:00-12:00, 12:00-15:00 and 15:00-18:00) as control factors because of the potential impacts of seasonality (Hill et al 2003) and the time of day (Post 1981) on baboon movement patterns. I used the identity of the animal as a random factor in analysis, to account for repeated measures on each individual, and for the maturation of individuals from one age-class to the next.

I transformed the dependent variable to meet the assumptions of the GLMM. On the basis of the distributions of the model residuals and the extent of heteroscedacity, the most appropriate transformations were log transformation (Lg^{10}) for the total distance travelled and inverse reciprocally cubed ($-1/x^3$) for the fractal dimension.

I used the Satterthwaite approximation such that the degrees of freedom vary across the tests due to variance in sample size across categories and the unbalanced design. I used robust estimations of covariances to allow for violations of model assumptions. Otherwise I set all models to the default linear model assuming a normal distribution with an identity link.

In the event of significant factor effects, I used post-hoc tests to determine which classes of individuals were significantly different from each other. As I made multiple comparisons I used the sequential Bonferroni method (Holm 1979) to reduce the potential for Type 1 errors.

5.3 Results

5.3.1 Distance travelled:

The mean distance travelled during 15 minute focal samples was 142.26 +-112.98 m (N=1128, range 3-723 m). The interaction between age and sex was significant, suggesting that the effects of age were different between the sexes (Table 5.3). Pair-wise comparisons indicated that there was a significant difference in the mean distance travelled between adolescent males and females (t=2.334, df = 14, p=0.035). There were no significant differences between any of the female age classes, but older juvenile males and adolescent males were significantly different to one another (t=-3.628, df=15, p=0.024, Figure 5.4).

The number of agonistic interactions received during the focal period had a significant effect on the distance travelled, with a coefficient of -0.082+- 0.030 (SE) suggesting that the distance travelled decreases as the count of agonism received increases. There was no significant effect of agonism given on distance travelled, with a coefficient of -0.012 +- 0.031 (SE). (Table 5.4).

Table 5.3: Results of a GLMM testing the influence of predictors on the total distance travelled during a 15 minute focal sample

	F	df1	df2	P
Model	**55.558**	**16**	**1111**	**<0.001**
Season	**48.638**	**3**	**638**	**<0.001**
Time	**41.988**	**3**	**459**	**<0.001**
Age	**8.949**	**4**	**17**	**<0.001**
Sex	0.236	1	4	0.654
Age * Sex	**10.173**	**3**	**3**	**0.044**
Agonism Received	**7.493**	**1**	**305**	**0.007**
Agonism Given	0.161	1	0	0.988

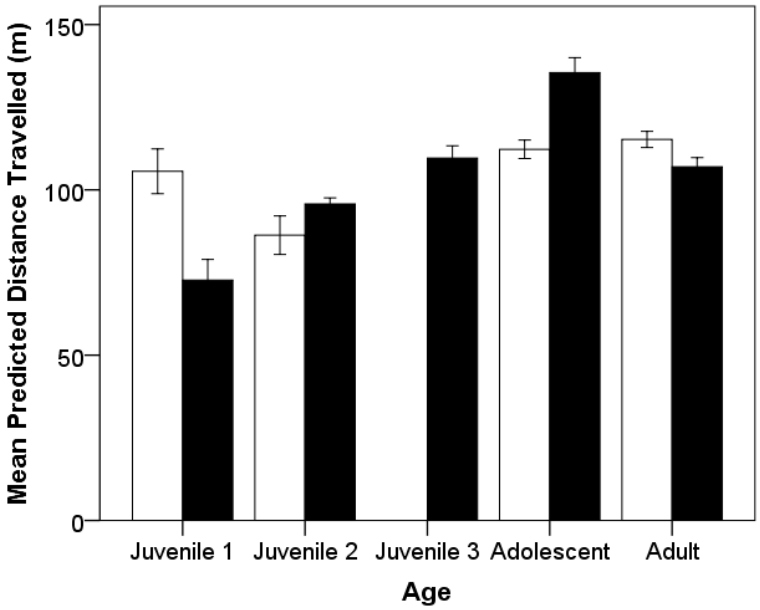

Figure 5.4: Mean +- SE predicted values for the total distance travelled during a 15 minute focal sample by age and sex. Predicted values are converted back from the log transformation. White columns indicate females, black columns indicate males.

5.3.2. Fractal Dimension

The mean fractal dimension of the travel paths was 1.223+-0.267 (N=1128, range 1-3.77). The interaction between age and sex was significant (Table 5.4), suggesting that the effects of age were different between the sexes. Pair-wise comparisons showed significant differences between male and female older juveniles (t=-4.729, df=2, p=0.039) and adults (t=-2.876, df=12, p=0.014), but no significant differences between ages within either sex (Figure 5.5)

The number of agonistic interactions received during the focal period had a significant effect on the distance travelled, with a coefficient of 0.019+-0.006 (SE) suggesting that as the count of agonism received increases, the fractal dimension of the travel path increases. The count of agonism given has no significant influence on distance travelled (coefficient of -0.007 +-0.007 (SE)).

Table 5.4: Results of a GLMM testing the influence of predictors on the fractal dimension a 15 minute focal sample

	F	df1	df2	Sig.
Model	**35.864**	**16**	**11**	**<0.001**
Season	**4.929**	**3**	**703**	**0.002**
Time	**34.642**	**3**	**353**	**<0.001**
Age	6.128	4	3	0.079
Sex	0.339	1	3	0.605
Age * Sex	**51.503**	**3**	**6**	**<0.001**
Agonism Received	**10.455**	**1**	**766**	**<0.001**
Agonism Given	1.095	1	0	0.990

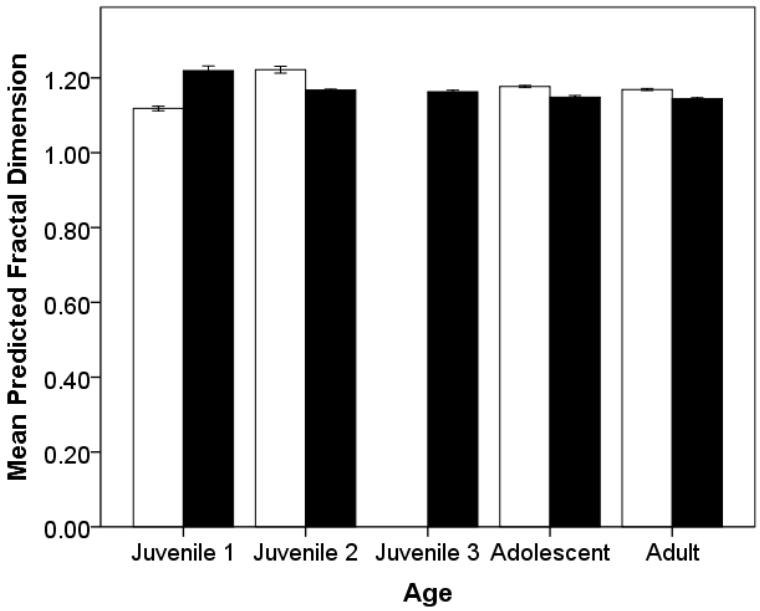

Figure 5.5: Predicted values +- 1 SE for the fractal dimension (D) of travel of a 15-minute focal observation by age. Predicted values are converted back from their $-1/x^3$ transformation. White columns indicate females, black columns indicate males. Error bars represent +- 1 SE

5.4 Discussion

In this chapter I assess the extent to which the movement patterns of individuals are affected by their age and sex, and the effects of agonism both received and given by a focal subject on their movements. While some of my predictions were supported, others met with limited support, and some were not supported.

I predicted that adult individuals would exhibit less tortuous paths than immature individuals, and that males and females paths would differ.. My results provide little support for these predictions as neither age nor sex alone were significant predictors of tortuosity. There is however support for sex differences between individuals of the same age classes, specifically older juveniles and adults. In these two age groups, female movement paths were significantly more tortuous than males, lending limited support to the prediction of sex differences in the tortuosity of movement, albeit only in two of the four age classes which contain both sexes. Sex differences should be expected in groups with high fission-fusion dynamics and segregation in ranging (e.g. chimpanzees (*Pan troglodytes*), where males patrol territorial boundaries and females forage separately, Bates & Byrne 2009; spider monkeys (*Ateles geoffroyi*) where males travel in subgroups while females forage separately, Fedigan & Baxter 1984, Chapman et al 1995). That they may also be a feature of primate groups that are generally considered more cohesive (King & Cowlishaw 2009) may indicate that sex differences in movement may be prevalent in primate groups, although few studies have as yet investigated differences in movement at individual levels (Bates & Byrne 2009). Females in this group were found to spend more time travel feeding (Chapter 3), and female primates in general may spend more time foraging and searching for food (Boinski 1988, Rose 1994), which may lead to more tortuous travel routes.

I also predicted that there would be sex differences in the distance travelled during a focal period.. My results provide only partial support for this prediction with males travelling significantly further than females, although this effect was only found among adolescent individuals. Adolescent males travelled further than adolescent females, and also further than older juvenile males. This pattern is consistent with male dispersal from the natal group into other surrounding groups (Altmann and Alberts 2003, Clarke

et al 2008), which generally occurs before the attainment of full adult stature (Alberts and Altman 1995). During adolescence, males are more likely to travel alone and further away from the rest of the group as they prepare for emigration. They are large and are therefore at a lower risk of predation and are also less likely to be engaged in consortship behaviour within the natal group than adult males, which may account for the increased travel distances found in adolescent males relative to the other age sex classes.

I also predicted that the direct amount of agonism given a focal animal will affect their movement paths, with increasing agonism leading to longer and more tortuous travel routes. While individuals who received more agonism had significantly more tortuous travel paths than those who received less agonism, contrary to my predictions and the findings of previous studies (African elephants (*Loxodonta africana*) Wittemeyer et al 2007, rhesus macaques (*Macaca mulatta*) Beisner & Isbell 2009), they also travelled shorter distances. However, as I predicted, the extent of agonism directed by the focal individual towards other group members had no effect on either tortuosity or travel distance. In this study group, exerting dominance over other group members appears to impart no cost to their own movement, but receiving agonism from others leads to constrained movement paths both in terms of a decreased ability to travel, and an increased tortuosity of travel routes. In addition to the multitude of benefits that high rank may confer (e.g. spatial benefits while foraging, Hall & Fedigan 1997; increased infant survivorship, Noordwijk & van Schaik 1999; higher reproductive output, Johnson 2003), a higher ranked individual is less likely to recieve agonism, affording them the capacity for travelling along more direct paths than other group members. Additionally, higher ranked animals may be more likely to direct agonism towards group members, with no cost to the efficiency of their own movement paths.

Rather than increasing their travel distance in order to obtain resources, it is possible that individuals that received more agonism may instead return to previously visited resources, as suggested by their increased fractal dimension. If an individual is displaced or supplanted from a feeding site, they will need to find alternative resources, which are likely to be less optimal (Janson 1985, Johnson 1989). Individuals may therefore employ a strategy of returning to previously visited feeding sites, including the site that the supplanting individual vacated, rather than searching further afield for new potential

sources of an unknown quantity or abundance. Returning to a partially depleted resource may provide greater assurance of calories at a lower energetic cost, which may account for both the decreased travel distance and increased tortuosity in individuals that received more agonism. While several studies indicate that the movements of chacma baboon groups as a whole exhibit properties suggestive of cognitive maps and prior knowledge of unseen resources (Noser & Byrne 2007, de Raad 2012) it is unclear how this affects individuals' movement within the group. Even if an animal in a group has knowledge of a valuable far off resource, they may be unlikely to move towards it by themselves this would place them at greater potential risk of predation or extra-group aggression. The best approach may therefore be to remain with the group as a whole, even if this requires feeding on less than optimal resources as a consequence of within-group competition. This will lead lead to shorter but more tortuous travel routes in animals which receive more agonism from other group members.

To date, few studies have addressed individual variation in primate movement. My results show that, despite living and moving together as a group, individuals in a chacma group vary in their movement patterns dependent on their age and sex, and the extent of social agonism received from other group members. The measures of movement I used in this study are two-dimensional, examining movement along only two axes of length and width. However, primates also inhabit a third dimension, height (Kimura 2002), which is particularly important for young juveniles (Chapter 3). I could not incorporate height above ground into either the distance travelled or the tortuosity of movement, because no measure of the fractal dimension as yet allows for three-dimensional coordinates. If height is included in both the distance travelled and measures of tortuosity, it is likely that due to their greater use of vertical space, young juveniles would appear to have longer, more tortuous travel paths. Future studies should aim to not only further examine individual variation in the movement of individuals in primate groups, but also the extent to which the use of height above ground affects both the distance travelled, and the tortuosity of movement.

5.5. Conclusions

In this chapter I show that the movement paths of individuals within a group of chacma baboons varies with their age and sex. I found sex differences in the tortuosity of movement in old juveniles and adults, with males exhibiting less tortuous routes than females. I also found that adolescent males travelled further than either old juvenile males or adolescent females. Finally, I found that the frequency of agonism received, but not given, by a focal subject affected movement. Individuals that received more agonism were found to have shorter, more tortuous routes than individuals that received less agonism. In the next chapter, I will further investigate the social environment of individuals, examining the social spacing and the extent to which the study group exhibits network assortativity by phenotype.

6 The Effects of Age and Sex on Social Spacing and Network Assortativity

6.1 Introduction

Being part of a group and being close to conspecifics have a wide range of benefits. From decreasing the risk of predation-related mortality (Janson 1990), increasing the potential for social learning of diverse skills (Lefebre 1995, Whiten 2000), to obtaining greater access to food resources through protection from within-group competition (Pereira 1988), having friends, particularly in high places, is an effective strategy to increase one's own chances of survival. Animals in groups are not distributed at random, with some forms of dyadic relationships being more attractive, and others avoided (Matsumura & Okamoto 1997), and kinship plays a major role in the patterns of associations in a primate group (Gouzoules & Gouzoules 1987, Silk 2002, Smith et al 2003). However, shared kinship alone does not fully explain the complex framework of relationships and associations that occur in primate societies. Importantly, there are conflicting forces of attraction and repulsion at work, requiring compromises to be made. Such compromises may be particularly important for immature animals as they balance the need for the acquisition of the skills necessary for growing into a successful adult while also meeting their energetic requirements and avoiding risks to their survival (Johnson & Bock 2004).

One of the major benefits of being close to other group members is the potential impact on the risk of predation. Having other group members nearby may increase the overall detection rate of nearby predators (Lazarus 1979), while it also allows each individual to reduce their own time spent being vigilant and spend more time foraging or engaging in other activities (Isbell 1994, Lima 1995). In the event that a predator manages to evade detection and launches an attack, an individual may increase its survivorship via the dilution effect by maintaining close proximity to a large number of neighbours (Foster

and Treherne 1981). The risk of death for each individual should be related to the number of neighbours in proximity, with the rate of attack per individual inversely proportional to group size (Turner & Pitcher 1986). Having close neighbours may also aid in foiling predation attempts by allowing for collective action such as mobbing which may act to deter or confuse a predator (Stanford 2002). Additionally, an animal's position in a group is considered to be a key predictor for mortality through predation (e.g. the selfish herd model, Hamilton 1971), and simulations suggest that predation risk is far greater on the periphery than in the centre of a group, and also higher towards the front of the group than to the rear (Bumann et al 1997). This suggests that an individual's position within a group will be constrained by their relative risks of predation such that the most vulnerable group members (e.g. adult females and their dependent offspring) will be positioned in the centre, while less vulnerable members (e.g. adult males) will be positioned at the periphery, and in particular at the front of a group (Washburn and Devore 1961, Rhine and Westland 1981).

Empirical studies of terrestrial and sexually dimorphic papionins have found some support for the suggested role of adult males as protectors through their non-random distributions among the group during progressions (e.g. yellow baboons (*Papio cynocephalus*), Rhine 1986; chacma baboons (*Papio ursinus*), Rhine et al 1985, Seuer 2011; mandrills (*Mandrillus sphinx*), Hongo 2014). Altmann (1979) argues that baboon progressions are random, and that situations in which adult males are overrepresented in the front or rear of the group are deviations from randomness in response to potentially dangerous situations. However, the fact that males appear to change their position in the group in such a responsive manner still suggests that adult males play a protective role. The number of males in multi-male, multi-female groups increases with predation risk (Hill & Lee 1998), and males are generally regarded as being more vigilant and active in defence against predators (Janson, in Isbell 1994), suggesting that associations with adult males are beneficial to other group members as a potential anti-predator strategy (Janson and van Schaik 2002). For example, juvenile baboons associate preferentially with adult males when predation risk is high (Rhine 1975, Rasmussen 1983).

Adult males have their own requirements to meet. Of these, reproduction is paramount and males can constitute a serious threat to infants as they seek to kill offspring that they have not sired and thus increase their chances of reproducing once the mother has resumed cycling (Hrdy 1977). As a response to the risk of infanticide, particularly from newly immigrated adult males, adult females may seek to form 'friendships' with existing adult males within the group (Smuts 1985, Palombit et al 1997, Palombit 2009). Such friendships persist in relationships with the offspring of the female friends, with males forming preferential attachments to juvenile offspring of former friends (Moscovice et al 2009). These preferred associations appear to be unrelated to actual paternity, and may instead be attributed to paternity uncertainty as a result of receptive females copulating with multiple males during their reproductive cycle (ibid.).

For animals to maintain proximity, social and ecological forces of attraction and repulsion require concessions or trade-offs to be made. While it may benefit all group members to remain close together to offset the potential risk of predation (Hamilton 1971, Rhine & Westlund 1981), this can lead to increased within-group competition for food, particularly in the case of clumped and patchily distributed food resources (Wrangham 1980, Boccia et al 1988, Barton et al 1996). There is little purpose in minimising predation-related mortality if other sources of mortality arise as a consequence, either through simple scarcity of resources leading to starvation (Southwick 1967), or through heightened levels of aggression and intra-group violence leading to wounding or even killing of conspecifics as they compete over valuable resources (Vogel et al 2007). Within-group competition can have an associated impact on spatial relationships among group members that go beyond vulnerability to predation (Barton 1993), although it is likely that spatial positions that favour reduced competition for resources may also be those that lead to greater vulnerability to predation (Ron et al 1996). Within-group competition and spatial position may also be mediated by factors beyond the distribution of resources or potential competitors, such as the energy and time invested in obtaining a resource (Shopland 1987), reproductive status (Busse 1984) and age (Van Noordwik et al 2002).

The close proximity of a younger, smaller, individual may be more tolerable to an older, larger animal as they will not yet represent a competitive threat for resources (Pereira 1988b). Given the reduced calorific requirements and slow growth rate of a juvenile primate, it is also likely that the younger animal will be able to still meet their requirements when foraging close to other group members, despite the increased competition for resources that they face (Janson and van Schaik 2002). Juveniles may sacrifice food intake in favour of spatial locations with reduced predation risk (Janson 1990), although they are also likely to maximise both safety from predation risk and food intake by preferring close adult neighbours that allow access to food (Pereira 1988b). However, as a young individual matures, the tolerances of both themselves and other group members are likely to decrease because they will require greater resources and can no longer afford to compromise their own calorific intake, and as their increased body size poses a higher competitive risk to others. For example, while an adult male may be likely to tolerate a young juvenile feeding in proximity, they are less likely to tolerate an older juvenile or adolescent male to feed nearby (Horrocks & Hunte 2002).

Several studies have indicated a degree of homophily or assortative mixing in primate associations, whereby individuals exhibiting similar characteristics such as rank, age, sex, personality or reproductive status form bonds with each other, likely due to commonalities in needs and experience (de Waal & Luttrell 1986, Matsumura & Okamoto 1997, Massen & Koski 2014, Carter et al 2015). Others have observed that relationships between immature group members exhibit similar patterns to those of their same-sex adult conspecifics (Cords et al 2010, Barale et al 2015, Kulik et al 2015). Juveniles are expected to try and form associations with other individuals on the basis of their own future success, therefore one of the key objectives for a juvenile will be to form beneficial social relationships that are likely to confer a competitive advantage (Fairbanks 2002).

The potential benefits offered by other group members will depend on the properties of the species-typical society. Juvenile females are expected to have stronger relationships with adult and other juvenile females than juvenile males do in a matrilocal group such as long-tailed macaques (*Macaca fasicularis*, van Noordwijk et al 2002),

while in a patrilocal group the opposite should be true and juvenile males' relationships with other males should be stronger than those of females (e.g. muriquis (*Brachyteles* spp.), Strier 2002). Male relationships with other males can, however, be of potential advantage even where males disperse as it is likely that males will encounter prior associates in the groups they immigrate into, or even immigrate into new groups together (Pereira 1988b, Fairbanks 2002). Several studies have indicated that in species exhibiting male dispersal, males immigrate into groups which contain individuals from the natal or other previous group (Walters 1987, Rajpurohit & Sommer 2002, Pines et al 2011). However, in baboon groups exhibiting strong male and female "friendships" (Smuts 1985, Palombit et al 1997), these associations have led to the suggestion that rather than being female-bonded, matrilocal societies, baboons actually represent cross-sex bonded societies (Byrne et al 1990). Although studies have found little support for this assertion (e.g. Henzi et al 2000, Henzi & Barret 2003), it is likely that given the wide variation in female and male bonding across ecological and social conditions (e.g. Barton et al 1996) that baboon groups represent a spectrum of social organisations in relation to male and female relationships.

Group-living primates may also benefit, or suffer, as a result of associations that they are not directly involved in. Support from conspecifics is an essential part of an individual's success (Gouzoules & Gouzoules 1987, Silk 2007, Silk et al 2009, Berghanel et al 2011), and polyadic interventions or policing behaviours act to maintain group cohesion and stability while de-escalating the risks of long-term aggression (Flack et al 2006). Primate societies are characterised by a high degree of post-conflict reconciliatory behaviour (Aureli 1997, Silk et al 1996, Silk 1997), meaning that even if two individuals engage in aggression, they and their kin are less likely to fully avoid or direct further aggression to each another in future encounters (Cheney & Seyfarth 1989, 1997, Cheney et al 1995). Such reconciliation is also effective if is directed by kin rather than the actors themselves (Cheney & Seyfarth 1999, Wittig et al 2007), therefore social relationships between individuals can be maintained indirectly in the absence of dyadic interactions. Such third-party interactions may lead to less assortative networks in group-living primates. If a conflict arises between two individuals, it may draw in other group members who otherwise may not normally associate with each other, for

example agonistic support by a mother against others behaving aggressively towards her infant (Silk 2007), paternal support of juveniles by adult males (Buchan et al 2003), and male support of a female friend against other group members (Lemasson et al 2008). Dyadic associations and interactions within a group may therefore occur not only the basis of individual preferences, but also on the basic of their shared relationships with other group members, potentially precluding a large demographically mixed primate group from exhibiting a strong degree of assortative mixing.

To date, no studies of primates have explicitly addressed the question of whether or not the patterning of agonistic and affiliative interactions among individuals in primate groups exhibit assortment by phenotype at a network level. A recent study examining assortative mixing in proximity and grooming networks found that assortativity was more common in grooming networks than in proximity networks, and that individuals that were phenotypically similar (rank, age, boldness and the propensity to generate and exploit information), or dissimilar (sex) were more likely to be associated with one another (Carter 2015). There was, however, high between-year variability, and the extent of assortativity was generally low. Examining the patterns of affiliative and agonistic interactions within primate groups may clarify whether or not primate groups exhibit assortative mixing beyond spatial associations or grooming relationships, along with expanding our understanding of the social pressures and priorities that group-living primates may encounter.

Aims and Objectives

In this chapter I will examine the effects of age and sex on social spacing and whether individuals interact with others within a group preferentially on the basis of phenotypic similarities. I aim to address several key predictions relating to intra-group spacing behaviour and the extent to which interactions with other group members exhibit assortative mixing. Using field observations of a multi-male, multi-female primate society, chacma baboons (*Papio ursinus*), I test whether there are age and sex related differences in intra-group spacing behaviour, whether social networks derived using different measures exhibit assortativity, and present a novel post-hoc method for

establishing the extent to which members of different age and sex classes exhibit preference or avoidance of associations with one another.

Spatial Relationships:

1) As a consequence of the potential anti-predation benefits afforded by proximity with other group members, along with the potential for a higher tolerance for within group feeding competition as a result of their reduced calorific needs, I predict that younger individuals will spend more time in close proximity with other group members than older group members do. I also predict that young juveniles will have a higher number of neighbours, and spend more time as part of a large group than older group members do. As body size increases with age, a concomitant reduction in both predation risk and tolerance of proximity by other group members will lead to older juveniles being more similar to mature individuals.

2) Given the matrilocal nature of chacma baboon groups, I also predict sex differences, with females spending more time in proximity to other group members than males. I also predict that females will have a larger number of neighbours and be part of a large group more often than males.

Network Assortativity

1) In a mixed age and sex chacma baboon society, I predict that phenotypically similar individuals will associate and interact with one another preferentially leading to assortative mixing. However, I predict that the extent of assortativity will be low, as the underlying nature of baboon societies precludes the possibility of complete assortment or disassortment in social networks as a consequence of individuals supporting others in varied contexts and the presence of cross-sex friendships.

2) Individuals in proximity and interaction networks will exhibit non-random patterns reflecting their different social priorities. Individuals are therefore likely to be close to and interact preferentially with others from whom they obtain the greatest benefit, and be less tolerant towards those that they benefit least from, or who may be direct competitors for resources. I predict that younger individuals will associate

preferentially with their older same-sex counterparts, and also associate preferentially with individuals similar in age. I also predict that pubescent and adolescents will interact with other individuals less than expected as they prepare to emigrate. Finally I predict that adult individuals will associate most with different sex counterparts, particularly in the case of males, and also exhibit decreasing tolerance in the form of increased aggression and responsibility for maintaining proximity with older juveniles.

6.2 Methods

6.2.1 Study site

I collected data over 19 months (November 2011 - June 2013) at Lajuma Research Centre in the Soutpansberg mountains, Limpopo Province, South Africa (29°26'05''E, 23°02'23''S). Further details on the study site can be found in the Methods chapter.

6.2.2 Subjects

The subjects for this study were a free-ranging chacma baboon group comprised of approximately 80 individuals. Information on group demography and the details of the study subjects can be found in the Methods chapter.

6.2.3 Data collection

I collected data via 15 minute continuous focal samples using the Observer XT package to design the data collection protocol, and Pocket Observer 3.0 installed on PSION Walkabout Pros. During these focal samples I collected data on the social spacing of the focal animal (distance and identify of their nearest neighbour, number of neighbours within a 5 m radius), along with all social interactions directed to or given by the focal animal (see Methods chapter for full data collection protocol). Due to difficulty in locating focal animals which were often spread widely through the landscape and in

dense vegetation, I was unable to collect data following a predetermined schedule. Instead, I collected data opportunistically, such that no animal was followed on more than one occasion in any given day, and that following a focal sample on a subject from one age and sex class, I sampled a different age or sex class. I also attempted to ensure that the data were distributed evenly through the day. Due to constraints in accessing and following the subjects, this proved problematic (see Methods chapter).

I collected a total of 418 hours of data on 55 focal individuals from different age and sex classes (Table 6.1). Of these individuals, 14 matured into an older age class during the study. I treated these demographic changes differently depending on the analysis (section 6.2.4).

Table 6.1: Description of data used in analysis. Total N = 69 (418 hours of observation, mean = 6.1 hours, SD = 5.3)

Sex	Age	N	Total hours	Mean hours per individual	SD
Male	Young Juvenile	2	5.49	2.75	3.53
	Old Juvenile	9	107.64	11.96	6.57
	Pubescent	5	33.53	6.71	3.44
	Adolescent	9	41.31	4.59	5.67
	Adult	11	54.52	4.96	4.69
Female	Young Juvenile	3	11.16	3.72	5.57
	Old Juvenile	3	13.50	4.50	4.72
	-	-	-	-	-
	Adolescent	8	69.69	8.71	5.28
	Adult	19	82.11	4.32	3.37

For full details of the data collection protocol, see the Methods chapter.

6.2.4 Data selection, treatment and analysis

i) Social Spacing

I used three variables to establish age and sex related differences in social spacing; the proportion of time spent within 5 m of another individual, the mean number of

neighbours when not in a large group, and the time spent as part of a large group. I calculated these variables as follows:

Proportion of time spent within 5 m of another individual

I collected data on the distance to the focal individual's nearest neighbour using different levels of proximity (time spent touching, not touching but within 2 m, 2-5 m, >5m and >10 m) as a proportion of total observation time minus any time spent out-of-sight or with an unknown distance to a nearest neighbour. In the majority of cases (6/10) the proportion of time spent at different proximities correlated significantly and negatively (Table 6.2). As a result, I combined all the categories within 5 m to ensure the independence of the analyses, resulting in the proportion of time spent within 5 m of another animal.

Table 6.2: Spearman rank correlations between the proportion of time spent within the different proximity categories of another animal. Significant values are bold, with exact p values in brackets. N=69 for all tests

	<2 m	**2-5 m**	**5-10 m**	**>10 m**
Touching	-0.182 (0.135)	**-0.340 (<0.004)**	-0.159 (0.193)	-0.175 (0.149)
<2 m	-	**-0.352 (0.003)**	**-0.677 (<0.001)**	**-0.350 (0.003)**
2-5 m		-	**0.328 (0.006)**	-0.135 (0.270)
5-10 m			-	**0.250 (0.038)**

Mean number of neighbours within 5 m when not in a large group

I used the proportion of total time (minus time spent out-of-sight, with an unknown number of neighbours, or with 10 or more neighbours) spent with x number of neighbours (where x = 0 - 9) within a 5 m radius to calculate the mean number of neighbours within close proximity when not in a large group. I excluded instances where an animal had 10 or more neighbours within 5 m from the total time because of the difficulty in accurately and rapidly counting large numbers of baboons. As a

consequence, the value presented here does not reflect the true mean number of neighbours. For this reason, I will also examine the time spent as part of a large group (10 or more neighbours) to assess the robustness of the mean number of neighbours.

Time spent as part of a large group

I used the time spent with 10 or more neighbours within a 5 m radius as a proportion of total observation time (minus time spent out-of-sight or with an unknown number of neighbours) as an indication of time spent as part of a large group.

Statistical Analyses

Due to demographic changes during the study period, several individuals are present in more than one age class. To control for this, I conducted GLMMs using individual identity as a repeated measure, examining the main effects of the age-class and sex of an individual and the interaction effect for the three target variables. All tests are two-tailed.

In the event of significant factor effects, I used post-hoc tests to determine which classes of individuals were significantly different from each other. As I made multiple comparisons (e.g. there are 10 (5*4/2) pairwise comparisons that can be made between the age classes), I used the sequential Bonferroni method (Holm 1979) to reduce the potential for Type 1 errors.

Finally, I conducted Spearman rank correlations on the three measures of social spacing to determine the extent to which they are related to one another.

ii) Assortativity

I created a series of directional social networks examining proximity, affiliation, agonism and proximity maintenance. I only included data in which both members of a dyad were identifiable. The youngest juveniles were difficult to identify quickly and accurately

during interactions in a complex habitat where visibility was often limited. I was often only able to record them as 'juvenile', or as 'juvenile male' or 'juvenile female'. As a result the individual-level data only represent 63% of the observed interactions involving young juvenile individuals. This loss of information affects all dyads, but is especially prevalent in interactions between young juveniles. I calculated the degree of loss for each age class as a proportion of total loss by taking the count of unidentified data for each age class and dividing this by the total observation time for that age class (Table 6.3). This means that while young juveniles are likely to be underrepresented in the datasets in general, they are especially underrepresented in dyads including other young juveniles, and conclusions relating to such relationships should be treated with caution.

Table 6.3: Proportion of dyads including unidentified young juveniles for each age class.

Age	Affiliative (%)	Agonistic (%)	Proximity (%)
Adult	24.55	6.62	13.53
Adolescent	16.19	11.20	16.03
Pubescent	0.00	23.60	17.68
Old Juvenile	8.90	14.46	12.96
Young Juvenile	50.36	44.12	39.80

I also excluded interactions with infants as they are not relevant to this study. I retained records that involve an interaction with an infant via its mother (e.g. I counted inspection of an infant by another animal if it involved an interaction with the mother, but not if it was in isolation away from the mother). As a result, the number of interactions included in each network are 1408 of 1695 (83%) affiliative interactions, 1672 of 1871 (89%) agonistic interactions, 2247 of 2532 (89%) approaches, and 1875 of 2062 (91%) departures. The focal animals spent a total of 290.42 hours within 5 m of other animals. Of this total, I excluded 59 hours of data because the identity of the nearest neighbour was unknown, meaning that that the final dataset represents 80% of the total data collected.

The resultant networks included 64 identified individuals (Table 6.4). I assigned individuals which matured from one age-class to another during the study to the class in which they spent the majority of the study period. As the data represent directional

relationships (i.e. the relationship A>B may not be the same as B>A), the number of dyads (edges) in the networks is 4032 (n*n-1=64*63).

Table 6.4: Sample size of age and sex classes for individuals within the networks. Total N = 64

Phenotype	N	Age	N	Sex	N
Adult Male	12	Adult	36	Male	32
Adult Female	24				
Adolescent Male	4	Adolescent	7		
Adolescent Female	3				
Pubescent Male	4	Pubescent	4	Female	32
Old Juvenile Male	8	Old Juvenile	8		
Young Juvenile Male	4	Young Juvenile	9		
Young Juvenile Female	5				

Network creation

I created four networks for use in analysis:

1) *Proximity*. I calculated the time that individual A spent with individual B as their nearest neighbour within 5 m as a proportion of the total observation time for A (minus time spent out-of-sight). As an individual's nearest neighbour is unlikely to be reciprocal (i.e. just because B is A's nearest neighbour, it does not follow that A is also B's nearest neighbour), this network is asymmetrical and derived from the focal animal's perspective.
2) *Affiliation*. I used the number of affiliative behaviours A directed to B, divided by the total observation time for A + observation time for B to create an hourly rate of affiliative behaviours A directed to B. See Methods chapter for the full ethogram.
3) *Agonism*. I used the number of agonistic behaviours A directed to B, divided by the total observation time for A + observation time for B to create an hourly rate of agonistic behaviours A directed to B. See Methods chapter for the full ethogram.
4) *Responsibility for maintaining proximity*. I pooled data on approaches and departures to and from 5 m, 2 m, and to within touching distance to calculate the rate of approaches and departures from A to B to create separate approach and departure networks. I used these networks to calculate the responsibility for

maintaining proximity using the Hinde Index (Hinde & Atkinson 1970, Martin and Bateson 1993):

$$\frac{A(a)}{A(b)+A(a)} - \frac{L(a)}{L(b)+L(a)} * 100$$

where A(a) is the rate of approaches A made to B, A(b) is the rate of approaches B made to A, L(a) is the rate of departures A made to B, and L(b) is the rate of departures B made to A. This index ranges from -1 to 1, so I scaled the values to fit a 0 to 1 range using feature scaling:

$$x' = \frac{x - \min(x)}{\max(x) - \min(x)}$$

where x is the original value and x' is the normalised value so that a value of 1 indicates that A is solely responsible for maintaining proximity, a value of 0 indicates that B is solely responsible for maintaining proximity, and a value of 0.5 indicates equal responsibility. Unlike the three other networks, in which a higher value indicates a stronger relationship and where A>B and B>A are not necessarily related, this network measures the strength of *asymmetry* in the relationship. An increase in the value of A>B leads to a decrease in the value of B>A as the dyadic value of A+B equals 1.

These networks are not truly independent of one another. For individual A to interact with individual B, they must be close to one another, thus the time spent together is likely to effect the dyadic interaction rate. Likewise, to get close to one another, either A or B must have approached the other, while an agonistic interaction may lead to a departure from proximity. However, I consider them independently as each network addresses a different aspect of social behaviour and the patterns of associations between individuals.

Analysis

Due to limitations in the original measure of assortativity (Newman 2002, 2003), previous studies examining assortativity in animal groups have tended to use binary measures for the relationships between dyads in which any association is scored as 1, and the absence of a relationship is scored 0 (Croft et al 2008), regardless of the strength of association or the number of times an interaction occurs between those individuals (e.g. Lusseau & Newman 2004, Wolf et al 2007). Weighted measures represent more powerful tools for network analysis than simple measures of occurrence (Whitehead 2008). As the networks I created are asymmetrical and represent the actual strength of relationships rather than the presence or absence of a relationship, I used the assortnet R package, that allows the analysis of weighted networks (Farine 2014), to test the effects of age, sex and age and sex combined on network assortativity in the four networks.

The assortnet package calculates the assortativity of a network based on the phenotypes of group members to determine whether associations occur more typically between similar or dissimilar individuals. Using weighted edges (values for the relationship between two individuals, or nodes, in the network) and discrete categorical phenotypes (age, sex, and age and sex), I developed mixing matrices where each cell indicates the value of the association that occurs in a phenotypic dyad (e.g. adult male aggression directed to adult females, proportion of time that old juveniles spent with pubescents as their nearest neighbours) as a proportion of the total observed associations. The assortativity coefficient *r* is calculated as:

$$r_d^w = \frac{\sum_i e_{ii}^w - \sum_i a_i^w \, b_i^w}{1 - \sum_i a_i^w \, b_i^w}$$

where e_{ii}^w is the proportion of the total network edge weights that occurs in nodes of type i, $a_i^w = \sum_j e_{ij}^w$ is the proportion of the total edge weights that starts at nodes of type I, and $b_j^w = = \sum_i e_{ij}^w$ is the proportion of the total edge weights that arrives at nodes of type j.

Values of *r* range from -1 to 1 where a value of 1 indicates a completely assortative network where similar phenotypes only associate with each other, 0 indicates a non-assortative network where similar phenotypes exhibit no preferences in associations, and where 0 to -1 is a completely disassortative network where similar phenotypes never associate. A completely disassortative network is closer to a randomly mixed network than a completely assortative network is (Newman 2003), therefore it is possible for such a network to fall within a -1 to 0 range, while a completely assorted network always provide a value of 1.

To determine the significance of *r*, Newman (2003) proposed using the jackknife method to calculate the standard error. The assortnet package gives standard error values for the *r* values it produces, but node permutations provide an equally good measure of the significance of the observed assortativity (Farine 2014, Farine personal communication). I therefore randomised each test 10,000 times by re-ordering the phenotypes of individuals in the network, retaining the underlying network structure. I then compared the observed *r* values against the randomised *r* values and classified the network as significantly more assorted than expected if the observed value was greater than more than 95% of the randomised values, and as significantly less assorted than expected if the value was smaller than 95% of the randomised values (i.e. I set significance thresholds to $p<0.05$, two-tailed).

Randomising the data also allows the assessment of whether the relationship between a phenotypic dyad indicates preferential association, an association that is no greater than expected, or avoidance. I compared the observed values for each cell in the mixing matrix (i.e. the value for each phenotype pair as a proportion of all values) against the same phenotype pairs in the randomised matrices to determine the significance of the association. Phenotypic dyads in which the observed values were higher than 95% of the randomised values indicate that the dyad was significantly more associated than expected and indicates a preferential association, while values lower than 95% of the randomised values indicate that the dyad was significantly less associated than expected, and therefore an avoided association.

6.3 Results

6.3.1. Spatial relationships

For the mean proportion of time spent within 5 m of any other group member (Figure 6.1a), the model as a whole was not significant ($F(8,60)=1.573$, $p=0.152$). The interaction between age and sex ($F(3,60)=0.090$, $p=0.965$) was not significant, nor was sex ($F(1,60)=0.199$, $p=0.657$). However, age had a significant effect ($F(4,60)=0.2730$, $p=0.037$). Post-hoc comparisons indicated that young juveniles spent more time within 5 m of other group members ($M = 89.92$, $SD=13.42$) than adolescents did ($M=70.61$, $SD=10.79$) ($t(60) = 3.227$, $p=0.020$).

For the mean number of neighbours within 5 m when not in a large group (Figure 6.1b), the model as a whole was significant ($F(8,60) = 3.216$, $p=0.004$). The interaction between age and sex ($F(3,60)=1.146$, $p=0.338$) was not significant, nor was sex (sex ($F(1,60)=2.034$, $p=0.159$). However, age had a significant effect ($F(4,60)=4.253$, $p=0.004$). Post-hoc comparisons showed that young juveniles had a higher mean number of neighbours ($M= 2.94$, $SD=0.95$) than all other age classes: older juveniles ($M=1.94$, $SD=0.54$; $t(60)=3.559$, $p=0.006$), pubescents ($M=1.91$, $SD=0.31$; $t(60)=2.9$, $p=0.036$), adolescents ($M=1.82$, $SD =0.56$; $t(60)=3.915$, $p=0.002$), and adults ($M=2.01$, $SD=0.56$; $t(60)=3.203$, $p=0.017$).

Finally, for the proportion of time spent in a large group (10 or more neighbours within 5m, figure 6.1c), the model as a whole was not significant ($F(8,60)=0.604$, $p=0.771$). Neither the interaction between age and sex ($F(3,60)=0.991$, $p=0.403$), age ($F(4,60)=0.415$, $p=0.771$) or sex ($F(1,60)=0.465$, $p=0.498$) were significant.

a)

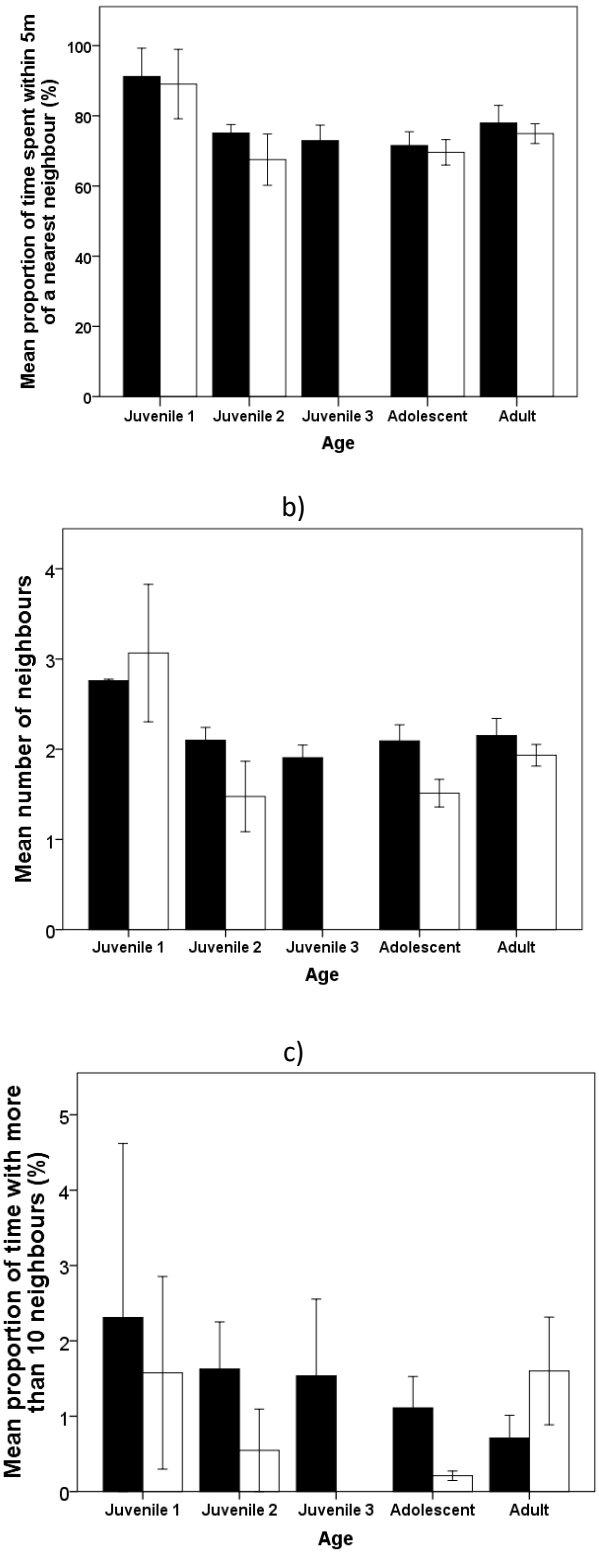

Figure 6.1: a) Mean +- SE proportion of time spent within 5m of another animal b) Mean number of neighbours within 5 m when not in a large group. c) Proportion of time spent with more than 10 neighbours within 5 m. Black columns = male, white columns = female. Juvenile 1 = Young Juvenile, Juvenile 2 = Old Juvenile, Juvenile 3 = Pubescent.

Correlations between variables

The proportion of time spent within 5 m of other animals was highly significantly correlated with the mean number of neighbours within 5 m when not in a large group (r_s = 0.701, p<0.001), but not with the proportion of time spent in a large group (r_s = 0.144, p=0.238; Figure 6.2), while the mean number of neighbours within 5 m when not in a large group was significantly correlated with the proportion of time spent in a large group (rs = 0.322, p=0.007).

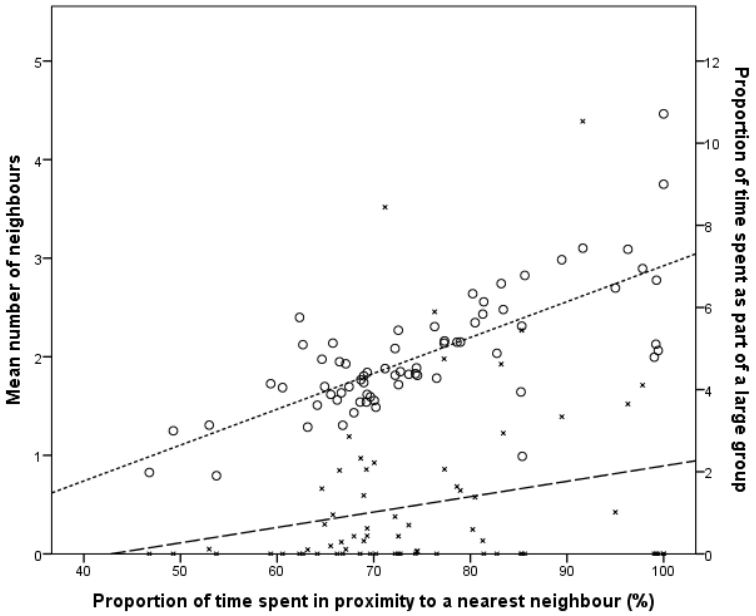

Figure 6.2 Mean number of neighbours within 5 m when not in a large group (open circles; small dashed line) and proportion of time spent in a large group (%, small crosses large dashed line) vs. proportion of time spent within 5 m of another animal

6.3.2. Network Assortativity

The assortativity coefficients created for the three different phenotypic conditions for the four networks (a total of 12 conditions) were generally close to zero (Table 6.5), indicating that this baboon population did not assort strongly based on age and sex and networks. However, the observed levels of assortativity were significantly higher in 8/12 (66%) of the conditions, and the observed assortativity was higher than any randomised value in 5/12 (42%) cases. Conversely, in 4/12 (33%) of conditions the observed coefficient was lower than the randomised values, although only one of these was

significant (sex-based associations in the affliative network). Only 2/4 (50%) of the networks were significantly assorted in the age and sex combined and sex only condition with an additional network being significantly less assorted in the sex only condition. All four networks were significantly assorted by age alone.

Table 6.5: Assortativity coefficients for the four networks along with p values relative to the phenotypically randomised networks

Network Type	Age and Sex		Age		Sex	
	r	**p**	**r**	**p**	**r**	**p**
Proximity	-0.0424	0.1514	**0.1044**	**0.0003**	-0.0995	0.0767
Affilation	-0.0109	0.3886	**0.1104**	**<0.0001**	**-0.1501**	**0.0091**
Agonism	**0.1559**	**<0.0001**	**0.1256**	**0.0004**	**0.3619**	**<0.0001**
Proximity Maintenance	**0.0576**	**<0.0001**	**0.0231**	**0.0023**	**0.1593**	**<0.0001**

i) Proximity

For the age and sex combined network (Table 6.6a), only 2/64 (3%) of the phenotypic dyads spent more time within 5 m of another animal than expected from the randomised networks: the proportion of time adult males spent with an adult female neighbour, and the proportion of time that adult females spent with adult males. Additionally, only 1/64 dyads (2%) spent significantly less time in proximity than expected, with young juvenile males spending less time with other young juvenile males than expected. In the age only network, only 1/25 (4%) of dyads spent more time in proximity (old juveniles and other old juveniles) (Table 6.6b). In the sex only network, none of the possible dyads spent more time in proximity than expected from the random networks (Table 6.6c).

Table 6.6: Mixing matrices for the proportion of time spent within 5 m of another animal for age and sex (a), age only (b), and sex only (c) networks. Values in bold indicate dyads that are significantly more associated compared to 10000 randomised distributions, and values in bold italics indicate dyads that are significantly less associated (p<0.05 * p<0.01, p<0.001***). AM = Adult Male; AF = Adult Female; AdM = Adolescent Male; AdF = Adolescent Female; Pb = Pubescent (male only); OJM = Old Juvenile Male; YJM = Young Juvenile Male; YJF = Young Juvenile Female.**

a)	**AM**	**AF**	**AdM**	**AdF**	**Pb**	**OJM**	**YJM**	**YJF**	**ai**
AM	0.0114	**0.1187*** **	0.0102	0.0231	0.0088	0.0145	0.0018	0.0048	0.1932
AF	**0.1167*** **	0.1175	0.0183	0.0226	0.0356	0.0401	0.0069	0.0091	0.3668
AdM	0.0093	0.0258	0.0069	0.0041	0.0032	0.0142	0.0033	0.0031	0.0701
AdF	0.0099	0.0173	0.0039	0.0015	0.0053	0.0082	0.0021	0.0032	0.0513
Pb	0.0063	0.0278	0.0077	0.0066	0.0035	0.0170	0.0011	0.0021	0.0721
OJM	0.0158	0.0380	0.0120	0.0107	0.0130	0.0410	0.0049	0.0061	0.1414
YJM	0.0029	0.0081	0.0093	0.0031	0.0024	0.0162	***0.0000**** **	0.0060	0.0478
YJF	0.0017	0.0377	0.0029	0.0030	0.0022	0.0069	0.0011	0.0016	0.0573
bi	0.1740	0.3909	0.0711	0.0746	0.0741	0.1581	0.0212	0.0360	1.0000

b)	**A**	**Ad**	**J3**	**J2**	**J1**	ai
A	0.3643	0.0742	0.0444	0.0546	0.0226	0.5601
Ad	0.0623	0.0164	0.0085	0.0225	0.0117	0.1213
Pb	0.0340	0.0143	0.0035	0.0170	0.0033	0.0721
OJ	0.0538	0.0227	0.0130	**0.0410***	0.0110	0.1414
YJ	0.0504	0.0182	0.0046	0.0230	0.0087	0.1050
bi	0.5649	0.1458	0.0741	0.1581	0.0572	1.0000

c)	**M**	**F**	ai
M	0.2367	0.2880	0.5246
F	0.2619	0.2136	0.4754
bi	0.4984	0.5015	

ii) Affiliation

For the age and sex combined network, 4/64 (6%) of the phenotypic dyads had a higher rate of affiliation than expected from the randomised networks (Table 6.7a). All of these dyads involved adult males. Adult males had higher rates of affiliation towards other adult males, adult females, and towards adolescent females, while adult females had higher rates of affiliation towards adult males. Meanwhile, 7/64 dyads (11%) had significantly lower rates of affiliation than expected from the randomised networks, with pubescent males interacting less with other pubescent males, and the remaining six instances all involving either young juvenile males (lower rates of affiliation directed towards adult males and other young juvenile males, and lower rates received from pubescent males), or young juvenile females (lower rates directed towards adolescent males and pubescent males, and lower rates received from adolescent males).

For the age only network, 3/25 (12%) of the dyads had significantly higher rates of interactions (adults directing affiliation towards other adults, adolescents directing affiliation towards adults, and old juveniles directing affiliation towards other old juveniles) while 3/25 (12%) had significantly lower rates (pubescents directing affiliation

towards other pubescents and young juveniles, and young juveniles towards pubescents) (Table 6.7b).

In the sex only network, 1/4 (25%) of dyads had significantly higher rates of interactions, while 1/4 (25%) had significantly lower rates of interaction, with males directing affiliation towards females at higher rates than expected, and females directing affiliation towards males at lower rates than expected (Table 6.7c).

Table 6.7: Mixing matrices for the rates of affiliative interactions for Age and Sex (a), Age only (b), and Sex only (c) networks. Values are in bold indicate dyads that interact at significantly higher rates compared to the 10000 randomised distributions, and values in bold italics indicate dyads that interact at significantly lower rates(p<0.05 * p<0.01, p<0.001***). AM = Adult Male; AF = Adult Female; AdM = Adolescent Male; AdF = Adolescent Female; Pb = Pubescent (male only); OJM = Old Juvenile Male; YJM = Young Juvenile Male; YJF = Young Juvenile Female.**

a)	**AM**	**AF**	**AdM**	**AdF**	**Pb**	**OJM**	**YJM**	**YJF**	ai
AM	**0.0305***	**0.1764*****	0.0103	**0.0282****	0.0013	0.0053	0.0028	0.0091	0.2639
AF	**0.0656***	0.1165	0.0195	0.0116	0.0153	0.0173	0.0047	0.0047	0.2552
AdM	0.0100	0.0637	0.0039	0.0095	0.0050	0.0039	0.0061	***0.0007****	0.1028
AdF	0.0102	0.0316	0.0051	0.0004	0.0064	0.0106	0.0034	0.0031	0.0708
Pb	0.0074	0.0369	0.0039	0.0119	***0.0000*****	0.0139	***0.0000*****	0.0009	0.0748
OJM	0.0055	0.0655	0.0031	0.0244	0.0143	0.0378	0.0065	0.0011	0.1582
YJM	***0.0000*****	0.0099	0.0056	0.0167	0.0006	0.0065	***0.0000*****	0.0044	0.0438
YJF	0.0028	0.0168	***0.0007****	0.0039	***0.0000*****	0.0016	0.0022	0.0024	0.0305
bi	0.1320	0.5173	0.0521	0.1066	0.0430	0.0970	0.0257	0.0264	1.0000

b)	**A**	**Ad**	**Pb**	**OJ**	**YJ**	ai
A	**0.3890***	0.0696	0.0166	0.0227	0.0212	0.5191
Ad	**0.1155***	0.0188	0.0114	0.0145	0.0133	0.1735
Pb	0.0443	0.0157	***0.0000*****	0.0139	***0.0009****	0.0748
OJ	0.0710	0.0275	0.0143	**0.0378***	0.0076	0.1582
YJ	0.0295	0.0270	***0.0006****	0.0081	0.0091	0.0743
bi	0.6493	0.1586	0.0430	0.0970	0.0521	1.0000

c)	**M**	**F**	ai
M	0.1843	**0.4592*****	0.6435
F	***0.1655*****	0.1910	0.3565
bi	0.3498	0.6502	1.0000

iii) Agonism

In the age and sex network, 5/64 (8%) of dyads showed a significantly higher rate of agonism than expected from the randomised networks (Table 6.8a). Most of these involve agonism directed by adult males, with rates of agonism towards other adult males, adult females, pubescent males and old juvenile males all higher than expected, along with pubescent males directing agonism towards adult females. Meanwhile, 8/64 (13%) of dyads showed significantly lower rates of agonism than expected, with adult and adolescent females, old juvenile males and young juvenile females directing less agonism towards adolescent males, young juvenile males and females directing less

agonism towards adult males, and young juvenile males directing less agonism towards other young juvenile males and pubescent and older juvenile males.

In the age only network, 2/25 (8%) of dyads showed higher rates of agonism than expected, with pubescents directing more agonism towards old juveniles, and old juveniles directing more agonism towards other old juveniles, while 1/25 (4%) of dyads indicated lower rates, with young juveniles directing less agonism towards pubescents (Table 6.8b).

For the sex only network, 1/4 (25%) dyads had higher rates of agonism, while 1/4 (25%) had lower rates, with males directing agonism towards females at higher rates, and females directing agonism towards males at lower rates (Table 6.8c).

Table 6.8: Mixing matrices for the rates of agonistic interactions for age and sex (a), age only (b), and sex only (c) networks. Values are in bold indicate dyads that interact at significantly higher rates compared to the 10000 randomised distributions, and values in bold italics indicate dyads that interact at significantly lower rates (p<0.05 * p<0.01, p<0.001***). AM = Adult Male; AF = Adult Female; AdM = Adolescent Male; AdF = Adolescent Female; Pb = Pubescent (male only); OJM = Old Juvenile Male; YJM = Young Juvenile Male; YJF = Young Juvenile Female.**

a)	**AM**	**AF**	**AdM**	**AdF**	**Pb**	**OJM**	**YJM**	**YJF**	ai
AM	**0.0742****	**0.0709***	0.0356	0.0125	**0.0418*****	**0.0388***	0.0018	0.0026	0.2782
AF	0.0033	0.1383	***0.0024****	0.0278	0.0051	0.0193	0.0103	0.0311	0.2376
AdM	0.0134	0.0255	0.0132	0.0043	0.0190	0.0344	0.0013	0.0042	0.1154
AdF	0.0006	0.0321	***0.0000*****	0.0028	0.0004	0.0018	0.0029	0.0042	0.0447
Pb	0.0046	**0.0438***	0.0047	0.0100	0.0093	0.0284	0.0032	0.0036	0.1077
OJM	0.0048	0.0446	***0.0005****	0.0225	0.0110	0.0560	0.0116	0.0079	0.1588
YJM	***0.0000*****	0.0028	0.0007	0.0020	***0.0000*****	***0.0009****	***0.0000*****	0.0213	0.0276
YJF	***0.0000*****	0.0160	***0.0000*****	0.0049	0.0004	0.0032	0.0007	0.0048	0.0300
bi	0.1008	0.3741	0.0571	0.0867	0.0870	0.1828	0.0318	0.0797	1.0000

b)	**A**	**Ad**	**Pb**	**OJ**	**YJ**	ai
A	0.2867	0.0783	0.0469	0.0581	0.0458	0.5158
Ad	0.0716	0.0203	0.0194	0.0363	0.0126	0.1601
Pb	0.0484	0.0147	0.0093	**0.0284***	0.0069	0.1077
OJ	0.0494	0.0229	0.0110	**0.0560***	0.0195	0.1588
YJ	0.0188	0.0076	***0.0004****	0.0041	0.0268	0.0576
bi	0.4749	0.1438	0.0870	0.1828	0.1115	1.0000

c)	**M**	**F**	ai
M	**0.4092*****	0.2785	0.6877
F	***0.0502*****	0.2620	0.3123
bi	0.4985	0.5015	1.0000

iv) Proximity Maintenance

In the age and sex network, observed asymmetries in responsibility for maintaining proximity were significantly different to the randomised networks in 12/64 (19%) of the phenotypic dyads (Table 6.9a). Adult males were significantly more responsible for maintaining proximity with other adult males, adult females, pubescent males and old

juvenile males, with pubescent males also being more responsible for maintaining proximity with adult females. Meanwhile, adolescent males and young juvenile females were both less responsible for maintaining proximity with one another than expected, with young juvenile females also less responsible for maintaining proximity with young juvenile males, while young juvenile males were themselves less responsible for maintaining proximity with other young juvenile males, and all other male age classes with the exception of adults.

In the age only network, significant assymetries were found in 2/25 (8%) of dyads, with some old juveniles being more responsible for maintaining proximity than other old juveniles, while young juveniles were less responsible for maintaining proximity with pubescents (Table 6.9b).

In the sex only network, 3/4 (75%) of dyads were asymmetrical, with some males being more responsible than other males, males being more responsible than females, and females being less responsible than males (Table 6.9c).

Table 6.9: Mixing matrices for asymmetries in responsibility for maintaining proximity for age and sex (a), age only (b), and sex only (c) networks. Values are in bold indicate dyads that are significantly more associated compared to the 10000 randomised distributions, and values in bold italics indicate dyads that are significantly less associated (p<0.05 * p<0.01, p<0.001***). AM = Adult Male; AF = Adult Female; AdM = Adolescent Male; AdF = Adolescent Female; Pb = Pubescent (male only); OJM = Old Juvenile Male; YJM = Young Juvenile Male; YJF = Young Juvenile Female.**

a)	**AM**	**AF**	**AdM**	**AdF**	**Pb**	**OJM**	**YJM**	**YJF**	ai
AM	**0.0491***	**0.0778****	0.0266	0.0216	**0.0351****	**0.0433****	0.0021	0.0021	0.2577
AF	0.0219	0.1172	0.0092	0.0300	0.0093	0.0305	0.0052	0.0172	0.2405
AdM	0.0127	0.0357	0.0070	0.0087	0.0170	0.0326	0.0026	***0.0021****	0.1184
AdF	0.0079	0.0331	0.0025	0.0049	0.0027	0.0028	0.0024	0.0066	0.0630
Pb	0.0028	**0.0525***	0.0026	0.0127	0.0056	0.0274	0.0042	0.0033	0.1111
OJM	0.0086	0.0691	0.0039	0.0253	0.0090	0.0386	0.0088	0.0130	0.1763
YJM	0.0021	0.0046	***0.0002****	0.0033	***0.0000*****	***0.0011****	***0.0000*****	0.0021	0.0134
YJF	0.0035	0.0053	***0.0007****	0.0032	0.0009	0.0024	***0.0007****	0.0028	0.0195
bi	0.1086	0.3953	0.0528	0.1097	0.0798	0.1787	0.0259	0.0492	1.0000

b)	**A**	**Ad**	**Pb**	**OJ**	**YJ**	ai
A	0.2660	0.0874	0.0444	0.0738	0.0266	0.4982
Ad	0.0894	0.0232	0.0197	0.0354	0.0136	0.1814
Pb	0.0552	0.0153	0.0056	0.0274	0.0075	0.1111
OJ	0.0777	0.0291	0.0090	**0.0386***	0.0218	0.1763
YJ	0.0155	0.0074	***0.0009****	0.0035	0.0056	0.0329
bi	0.5039	0.1624	0.0798	0.1787	0.0752	1.0000

c)	**M**	**F**	ai
M	**0.3432****	**0.3339*****	0.6770
F	***0.1026*****	0.2204	0.3230
bi	0.4985	0.5015	1.000

6.4. Discussion

In this chapter I assessed the extent to which age and sex influence spatial relationships in a group, and whether the observed patterns of social associations and interactions among group members indicate assortative mixing according to three different levels of phenotypic categorisation. The results support several of my predictions, while others received mixed or no support.

Spatial Relationships

The results support my prediction that there are age-related differences in social spacing in a baboon group evidenced by differences in the mean number of neighbours within 5 m when not in a large group. The results do not, however, support my predictions that there will be age differences in the proportion of time spent in proximity to other group members, or as part of a large group. Nor do the results support my prediction that there will be sex differences in social spacing, with no sex differences, and no interaction between age and sex in any measure of social spacing.

While I found no age or sex differences in the proportion of time spent as part of a large group (10 or more neighbours within 5 m), this provides support that the mean number of neighbours is a robust indicator. Due to the difficulty in counting a large number of baboons, I used a large group category to ensure that the mean number of neighbours when not in a large group was accurate. If I found significant differences in the proportion of time spent in a large group, this would suggest that the mean number of neighbours may be an inaccurate representation. However, as no differences were found, and because of the significant linear relationship found between the mean number of neighbours and the proportion of time spent in a large group, I am confident that the mean number of neighbours I used in analysis is a reliable measure, albeit it one that may be a slight under-representation of the true mean.

The youngest juvenile class had more neighbours within 5 m when not in a large group than all other age classes. Young juveniles had approximately one additional neighbour than older individuals, while the older classes showed no significant variation in the

mean number of neighbours. This finding is consistent with the hypothesis that younger, more vulnerable animals position themselves within a group in such a way that they maximise survivorship in the event of predation (Janson and van Schaik 2002). One more neighbour in close proximity should both act to deter potential predators, and reduce the risk of any one individual's mortality in the event of an attack (Turner & Pitcher 1986). The presence of an additional neighbour disappears in older juveniles having no more neighbours than adults, suggesting that predation risk may decline with age and body size, but also that the trade-offs required to have more neighbours become unsustainable. While a younger, smaller individual may still be able to meet their calorific requirements with more animals in proximity, an older individual may be unable to do so, or, importantly, may not be tolerated in proximity by other group members, as they now constitute a greater potential for competition (Pereira 1988b). Effectively, the benefits that may be afforded by more neighbours are out-weighed by the costs as individuals mature, both to the individual itself and to other group members.

There is, however, an alternative possible explanation for the higher number of neighbours in the youngest juveniles relative to older group members. Previous studies have suggested that young juvenile primates have preferential associations with their mothers, and may spend more time close to them (e.g. yellow baboons (*Papio cynocephalus*) Pereira 1988b; long-tailed macaques, (*Macaca fasicularis*) Noordwijk et al 2002; blue monkeys (*Cercopithecus mitis stuhlmanni*), Cords et al 2010). If that is also the case in this study population, then in the event of their mother having a new dependent offspring, a preferred association with the mother will lead to an association with their young sibling. Additionally, juvenile females are also attracted towards lactating females to gain access to the infant and practice their own maternal skills (Hrdy 1976, Silk 1999, Fairbanks 2002), thus attraction towards an infant may inflate the number of neighbours in proximity. My study only included the identity of the nearest neighbour along with the number of neighbours within 5 m, rather than the identities of all individuals within 5 m. Additionally, due to the absence of long-term observations at my field site, genealogies are unknown and it is not possible to determine the role of mothers and their dependent offspring in the elevated number of neighbours in the young juveniles of this study.

Female primates in general exhibit marked attractions to other females with infants (Silk 1999, Silk et al 2003), but I found no sex differences in any of the three measures of social spacing. The lack of such sex differences does not support my hypothesis that females will have stronger spatial bonds with other group members, and indicates that the age-related differences I observed are robust. If the mean number of neighbours is affected by proximity to lactating females and their offspring, then, given the greater attraction of females to such mothers, juvenile females should have more neighbours than juvenile males. There is no evidence for such a difference, so the most parsimonious explanation for the age-related differences I report is that young juveniles do indeed position themselves in places of greatest safety relative to older individuals.

Network Assortativity

The network assortativity results broadly support my prediction that baboon societies exhibit assortative mixing by phenotype in their associations and interactions with one another. Assortment was more prevalent among the networks and treatments than disassortment, and in the majority of cases the observed levels of assortment were significant. However, the patterns of assortment varied with phenotypic category, with age exhibiting the most consistent pattern of assortment, indicating that individuals of similar ages are likely to be in proximity and interact both agonistically and affiliatively, and that there are also asymmetries in their responsibility for maintaining proximity. The other two phenotypic categories exhibited greater variation in assortment between the networks. In the sex only condition, agonism is more prevalent between individuals of the same sex as are asymmetries in proximity maintenance, while affiliative interactions are more prevalent between individuals of different sexes, and proximity being more or less random and unassorted. For individuals of similar ages and sexes, the proportion of time spent in proximity and rates of affiliation were random, and assorted for both rates of agonism and asymmetries in proximity maintenance.

The results also support my prediction that while the networks will show assortment by phenotype, the extent of assortativity will be low. Considering that a fully assorted network in which only individuals of the same phenotype interact or associate with one

another would generate an assortativity coefficient, *r*, of 1, with a value of 0 indicating a randomly mixed networks (Newman 2002, 2003), the assortativity coefficients are all closer to a random than fully assorted network or disassorted network. Despite the low assortativity coefficients, in the majority of cases these coefficients were higher than those calculated via randomising the phenotypes of individuals, indicating that these networks were significantly more assorted than expected. These findings are similar to the only other study that has examined phenotypic assortativity in weighted networks in primates (Carter et al 2015). While their study used more phenotypes relating to social information use and personality types, they also used age and sex, and created assortativity measures for two groups of baboons across 6 years. For grooming networks they found that assortativity for age ranged -0.196 - 0.176 and values for sex ranged -0.332 - 0.263, while for proximity networks values for age ranged -0.058 - 0.213 and values for sex ranged -0.217 - 0.076. In general, they found that grooming networks were significantly assorted by age (7/8 networks) and sex (7/8 networks), but that proximity networks were less assorted by sex (4/8 networks) and age (2/8 networks). I found that proximity was affected more by age than sex. These suggest that further research is required to determine the effects of age and sex on proximity networks in baboons, and indeed other primate species.

Due to the difficulty in identifying the youngest juveniles in interactions, it is possible that the assortativity coefficients I have presented do not truly reflect the actual networks among the group members. This possible sampling bias is particularly important for the post-hoc comparisons I conducted to test the hypothesis that interactions and associations between phenotypes will reflect the social priorities of the interacting individuals. The removal of unidentified individuals had the largest impact on associations between young juveniles, meaning that in some cases the mixing matrices indicated that these individuals never interacted. These phenotypic dyads would therefore appear to be significantly avoided relationships, but this is an artefact of the necessity to include only identified individuals. As a result, I focus my discussion on the other phenotypic dyads.

The results offer some support for my prediction that associations and interactions between phenotypic dyads are non-random and serve to benefit the interacting individuals. I predicted that younger individuals will associate preferentially with older individuals of the same sex, and with individuals of the same age. The mixing matrices indicated that older juveniles had stronger than expected relationships with other older juveniles. They spent more time in proximity and had higher rates of both affiliative and agonistic interactions with one another than expected, while also exhibiting greater asymmetries in the responsibility for maintaining proximity, indicating that same age peers are important relationships in older juvenile baboons (see also Cheney 1977 for homophily in play behaviour in juvenile baboons, Periera 1988, 1989 for agonistic development in baboons). They did not, however, associate preferentially with older same sex individuals, and avoided directing agonism towards adolescent males. This older juvenile category is compromised solely of males; although there were several older juvenile females at the onset of my data collection, they all reached menarche early on and were subsequently classed as adolescents for the majority of my study.

I also predicted that pubescent and adolescent males would generally associate less with all group members as a result of their preparations for emigration. In the majority of cases, the mixing matrices for these phenotypes were no higher or lower than expected on the basis of the randomised matrices. Pubescents appeared to avoid affiliative interactions with one another, while directing more agonism towards and being more responsible for maintaining proximity with adult females than expected by chance, while adolescent males exhibited no preferences in any network. These males can therefore not be considered as asocial, but their interactions with other group members are generally non-differentiated. Considering that the adolescent males in this study spent less time with other group members in general (see also Alberts & Altmann 1995), they may simply have less opportunities for interactions with other group members.

Finally, I predicted that adults would associate preferentially with adults of the other sex, and exhibit intolerance towards other group members, particularly older juveniles. The results indicated that adults did show preference towards different sex adults, with adult males and adult females spending more time in proximity and with higher rates of

affiliation than expected, with adult males also directing more affiliation towards adolescent females. Adult males also directed affiliation towards other adult males at higher rates than expected. While this may seem surprising, considering the heightened risk of wounding in the event of violent encounters between adult males (Drews 1996), higher than expected rates of affiliation may prevent or de-escalate violence. Conversely, as predicted adult males directed more agonism than expected towards pubescent and older juvenile males, and were more responsible for maintaining proximity with them, showing a decreased tolerance to older immatures (Horrocks & Hunte 2002). Adult males appear to tolerate only adult females close to them, and actively keep other group members away from proximity through a combination of increased agonism towards them, and a lack of affiliative overtures. Adult females, in contrast, exhibited higher than expected rates of affiliation with adult males, but generally interacted with other classes no more or less than expected.

My results indicate that adult males are disproportionately represented in the interaction networks of chacma baboons. I found them to consistently interact not only among themselves, but also with other age classes at higher than expected rates, particularly with regards to agonistic interactions. They are also more responsible for maintaining proximity with other group members. With regards to immature group members, adult males appear to represent a significant competitive threat, directing agonism towards both old juveniles and pubescents at higher than expected rates. The underlying multi-male multi-female structure of chacma baboon troops and the presence of multiple adult males may therefore pose problems for younger group members. These interactions between adult males and other group members warrant further investigation in terms of the potential conflict for resources that these associations may entail.

6.5. Conclusions

I found that patterns of social spacing in a chacma baboon group differ by age, but not sex, with young juveniles having approximately one more neighbour within 5m when not in a large group than older individuals did. However, I found no differences in terms

of either the time spent in proximity (within 5 m) of other group members, or the time spent as part of a large group (more than 10 neighbours within 5 m). I also found that social networks derived from proximity, rates of affiliation, rates of agonism and the responsibility for maintaining proximity exhibit varied degrees of assortativity by age, sex, and age and sex. The most consistent finding is that all networks were significantly, albeit weakly, assorted by age. Finally, by using a novel approach to network randomisation, I found that the patterning of associations and interactions between phenotypic dyads is non-random, and reflects the priorities and tolerances of the individuals in a group. Adult males are especially important in these networks, directing more agonism and being more responsible for maintaining proximity to other group members than other group members are.

7. Discussion

My primary aim with this study was to examine age and sex related differences in primate behaviour, with a specific focus on differences between juveniles and other age classes that live in the same social group. In contrast to other mammalian orders, a major feature of primate groups is that they exhibit year-round associations between males and females, with 73% of primate genera exhibiting such associations, far exceeding the proportion found in any other order (van Schaik & Kappeler 1997). Primate groups are generally composed of three or more mixed-sex adults and their dependent offspring (Kappeler & van Schaik 2002). The juvenile period may thus be an adaptation to the pressures that obligate group-living entails, both in terms of social (e.g. Joffe 1997) and ecological (e.g Janson & van Schaik 2002) pressures.

To meet this aim, I conducted a 19 month field study on a wild group of chacma baboons, taking a multi-faceted approach to investigating age and sex related differences in a variety of contexts. In this discussion chapter, I first present a summary of the key findings from my research before reflecting on some limitations of my study. I then present the broader implications of my findings in the context of our understanding of the juvenile period in primates, before providing recommendations for future research.

7.1. Summary of Findings

In chapter 3 I used data collected via scan sampling to examine the effects of age and sex on activity budgets, examining the proportion of time engaged in activities, the proportion of time spent at different heights, and the proportion of time engaged in activities either on, or above the ground. I found significant differences in the proportion of time spent resting (characterised by adolescent and adult males spending more time resting than other age and sex groups, and also a positive correlation between body size and the proportion of time spent resting). I also found differences in the proportion of time spent travel feeding (with adult females spending more time travel feeding than young juveniles or pubescents), but no differences in the proportion of time spent

moving. Although, similar to previous reports (Post 1980), young juveniles spent more time feeding that adults (135% of the time of adult females, and 129% of the time as adult males), these differences were not significant. This is contrary to the prediction that young juveniles should be less efficient or capable at acquiring food (Janson & van Schaik 2002). I also found significant differences in the time spent engaged in social activities (although pairwise comparisons were only significant between adolescent males and females), and, perhaps more importantly, significant differences in the types of social activities the age sex classes engaged in. Play was highest in the youngest juveniles, and declined with age until virtually absent in adults (see also Owens 1975, Fagen 2002), while grooming was the most prevalent activity for all other classes, particularly adult females (see also Mitchell & Tokunaga 1976, Seyfarth 1977 Thierry et al 1990, Henzi & Barratt 1999).

While all age and sex classes were predominately terrestrial, the youngest juveniles spent significantly less time on the ground than adolescent and adults of both sexes, and more time 2-5 m from the ground than adults of both sexes. As body size increased, individuals spent more time on the ground, and less time at 2-5 m, suggesting that young juveniles are better able to use resources or refuges above the ground than are older and larger individuals (Menard 1985, Menard & Vallet 1986). Predation pressure from aerial predators is likely to be low for this population, allowing individuals to use vertical space at little risk. Young juveniles spent significantly more time feeding above the ground than adolescents and adults of both sexes, with time spent feeding above the ground being negatively related to body size. Thus, while there were no significant age or sex related differences in the total proportion of time spent feeding, the youngest and smallest individuals obtained more of their food from sources above the ground than adult females or adult males. The relatively small size of juveniles may allow them to meet their calorific requirements via food sources free from direct competition with other, larger, group members.

In Chapter 4 I examined the extent to which the baboons exhibited behavioural synchrony (Engel & Lamprecht 1997, Raussi et al 2011, Asher & Collins 2012). I used the Kappa coefficient of agreement (Fleiss 1971, Siegel and Castellan 1988) as my indicator of behavioural synchrony due to its robust ability to control for expected levels of

synchrony based on the distribution and prevalence of behaviours (Asher & Collins 2012). In addition to examining the extent of behavioural synchrony of the whole group, I also partitioned the data into an immature only group comprised of young and old juveniles and pubescents, and a mature group, comprised of adolescents and adults. I also assessed the effects using different numbers of behavioural categories (two, five and 10 behaviours), and the effect of including whether a behaviour took place on, or above the ground on behavioural synchrony. All measures of behavioural synchrony indicated low, but significant levels of synchrony (rated as 'slight' (Landis & Koch 1977) or 'poor' (Fleiss 1981) agreement). Additionally, the Kappa values generated in these analyses suggested that the relationship between the number of categories used in the determination of behavioural synchrony is not as straight-forward as previously reported (Asher & Collins 2012), and that increasing the number of behavioural categories (including in my case the addition of height above ground) does not necessarily lead to a reduction in behavioural synchrony.

Behavioural synchrony was higher both in the mature-only group and the immature-only group than for a group containing all animals, confirming previous research indicating that individuals that are more similar in size have higher levels of synchrony (Ruckstuhl 1999, Aiwaz & Ruckstuhl 2011, Foerder et al 2013). However, by randomizing individuals to either the immature or mature group (while retaining the number of individuals within each scan and the behaviours of individuals) I found that while the observed behavioural synchrony of the mature-only group was significantly higher than random groups, the immature-only group was no more or less synchronised. This asymmetry suggests that the behavioural synchrony of mature animals may be compromised by the presence of younger individuals. The low levels of behavioural synchrony found in all conditions, however, suggests that chacma baboon groups are able to remain cohesive although group members engage in different behaviours at the same time. Unlike species in which sex differences in activity budgets lead to segregated groups (e.g. ungulates, Ruckstuhl 1998, Michelena et al 2006), primate groups may be resilient against individual variation in activity, affording juveniles time to engage in behaviours specific to their own social and ecological development.

In Chapter 5, I examined the effects of age, sex and social dominance on the movement paths that individuals took through the landscape. I found that individuals travelled 142.26 +-112.98 m (N=1128, range 3-723 m) in a 15 minute period, and found a significant interaction between the age and sex of an individual and the distance they travelled. Adolescent males travelled further than both adolescent females and old juvenile males, and I attributed this difference to be a result of male dispersal in baboons (Altmann and Alberts 2003, Clarke et al 2008).

I also found differences in the fractal dimension of travel routes and a significant interaction between the effects of age and sex. Male adults and old juveniles had significantly lower fractal dimensions than their female counterparts, suggesting that females follow more tortuous travel paths than do males. Meanwhile, no differences were found between any same-sex age classes. These sex differences are likely to be a result of the greater time that females spend travel feeding and searching for food (Chapter 3, Boinski 1988, Rose 1994). Sex differences in movement that are more commonly associated with fission-fission dynamics (Bates & Byrne 2009, Chapman et al 1995) may therefore also be present in species such as chacma baboons that move together as more cohesive units (King & Cowlishaw 2009).

I also found that agonism had a significant effect on both tortuosity of movement and the distance travelled. Individuals that received more aggression travelled more tortuous paths, but contrary to my predictions and the findings of previous studies (Wittemeyer et al 2007, Beisner & Isbell 2009), travelled shorter distances than individuals who received less agonism. However, there was no significant effect of aggression given on either distance travelled or tortuousity of movement. Effectively, exerting aggression comes at no cost to an individuals' movement patterns, while receiving aggression from other group members constrains an individuals' movement.

Finally, in Chapter 6 I examined the extent to which age and sex affect the social spacing of individuals, and the degree to which individuals within the group exhibit phenotypic assortativity and homophilic preferences in their social networks. While I found no differences in either the proportion of time spent within 5 m of other individuals when not in a large group or time spent as part of a large group (10 or more neighbours within

5 m), I found that age had a significant effect on the mean number of neighbours within 5 m when not in a large group. The youngest juveniles had approximately one more neighbour than any other age class (2.94 +- 0.95 neighbours compared to between 1.82 +- 0.56 in adolescents and 2.01 +- 0.56 in adults). This is consistent with the hypothesis that younger, more vulnerable animals position themselves among the group to maximise survivorship in the event of predation (Janson & van Schaik), and that older individuals may tolerate the proximity of young juveniles more than that of larger animals (Periera 1988b). The benefits of being in proximity to more individuals likely outweigh the costs in young juveniles, but these trade-offs appear to be less beneficial for older individuals.

In examining the extent of phenotypic assortativity in weighted social networks (Farine 2014, Carter et al 2015) derived from different measures (the time spent within 5 m of another individual, the rates of affiliative and agonistic interactions, and the responsibility for maintaining proximity with other group members), I found that networks were more likely to be assorted by age than by sex, or age and sex combined. While the majority of networks showed assortment by phenotype, this extent of assortativity was low, with the highest level of assortativity found (0.3619) in sex-only agonistic networks. A fully assorted network would have a value of 1, with values closer to zero indicating random assortment (Newman 2002, 2003). However, despite these low assortativity coefficients, the majority of networks were more assorted than networks in which the phenotypes of individuals were randomised, suggesting that the networks are more assorted than would be expected by chance.

I also presented a novel method of assessing whether phenotypic dyads preferred or avoided associations with one another through comparing the observed prevalence of associations against those produced by randomising individuals' phenotypes (Farine 2014, *personal communication*). While the majority of phenotypic dyads in the networks associated no more or less than expected, in other cases the patterning of associations and interactions was non-random, reflecting the priorities and tolerances of the interacting individuals. Adult males were found to be particularly important within the networks, directing more aggression towards, and being more responsible for, maintaining proximity with other group members, particularly with older juveniles and

pubescent males, indicating a decreased tolerance to these groups (Horrocks & Hunte 2002). I also found that older juveniles had stronger than expected relationships with other older juveniles, spending more time in proximity with one another, interacting at higher rates for both affiliative and agonistic behaviours, and exhibiting asymmetries in their responsibilities for maintaining proximity. Same age peers are important social partners for juvenile baboons (see also Cheney 1977, Pereira 1988, 1989), but juveniles did not appear to preferentially associate with same-sex older peers.

7.2. Limitations of the study

There are three important and interconnected limitations to my study: the problems I had accessing and following the baboons consistently, the lack of juvenile females in the study group, and the under-representation of young juveniles in focal samples relative to their prevalance in the group.

The first of these limitations means that both my scan samples and focal samples were unevenly distributed throughout the day, with few samples collected between 11:00 and 14:00. My data were also unevenly distributed spatially, with little to no data collected in some areas of the study group's range. The inability to consistently follow the study group into certain areas also means that I lacked the data to produce accurate estimations of daily travel routes and home range estimates and to place the findings of Chapter 5 within a wider spatial context.

The second limitation was the lack of juvenile females in the study group. While the sex ratio of the younger juveniles was relatively equal, the older juveniles were predominantly male. All of the older juveniles that were female became adolescents during my study, with two doing so in the first few months. Although this means that I have a good sample of adolescent individuals, ranging from these young females starting to cycle to older individuals entering their first pregnancy, it limits the inferences I am able to make relating to juvenile females. This particularly affects comparisons between male and female juveniles, and female juveniles relative to their older same-sex

counterparts. Additionally, I included a male-only age class (pubescence) due to the later age at maturity found in males relative to females. These pubescent males represent a transitional stage, as they are larger than and outrank all adult females (personal observation), but are not yet part of the adult male hierarchy, and are non-reproductive. The absence of a matching life history stage for females, and the general lack of females in the older juvenile category may mean that my results are unbalanced, particularly in terms of the interaction between age and sex present in the GLMMs in chapters 5 and 6. While variation in animals within age sex classes is to be expected in natural systems, the impacts could only be overcome by studying multiple groups. This is beyond the scope of a PhD study given the sizes of the baboon groups in the Soutpansberg Mountains and the difficulty in habituating new groups in the study area.

The final major limitation, the lack of representation of young juveniles in focal samples, reflects the difficulty of observing small, unpredictable individuals in a complex environment. While my attempts to focal older juvenile or adolescent and adult individuals were largely successful, many of my attempts on young juveniles failed within the first few minutes of the focal sample. Young juveniles were prone to engage in energetic play with one another, meaning that not only was it difficult to accurately identify the focal subject in a rapidly moving throng of very similar individuals, but that they also chased one another up trees or into dense vegetation. Also, while the majority were well habituated to a static observer, they were less willing to allow me to follow them once moving, and often ran away. Rather than place these juveniles under unnecessary stress from repeated attempts at observations, I selected focal subjects more amenable to observation following an abandoned focal sample. Fortunately, it was possible to collect scan samples on the young juveniles, so they are well represented in the analyses I presented in Chapters 3 and 4. The two chapters reliant upon focal sampling data (Chapters 5 and 6) are however constrained by the amount of data I was able to collect on the youngest juveniles.

7.3. Juvenile primates in a group context

The challenges that juveniles' face and their behavioural priorities are different to those of adults (O'Brien & Kinnaird 1997, Janson & van Schaik 2002, van Noordwijk et al 2002). Juvenile primates must engage in activities both vital for survival to adulthood, and for subsequent success as an adult (Pereira 1988b). By living in groups, individuals may enhance their immediate survival through decreasing the risk of predation-related mortality (Foster & Treherne 1981, Turner & Pitcher 1986, Janson 1990). Group living also allows for the social learning of skills, both ecological (Rapaport & Brown 2008, Jaeggi et al 2010) and social (Poirier & Smith 1974, Periera 1988a, Barale 2015) that are vital for survival. However, group living also comes at a cost (Majolo 2008), and increasing group size will lead to more within-group competition for resources, particularly food (Wrangham 1980, Isbell 1991, Janson & Goldsmith 1994).

Juveniles may be limited in their ability to compete with older, larger and more experienced group members (Rubenstein 2002). Juvenile foraging competence and abilities at acquiring and processing foods may be lower than that of adults (e.g. van Schaik & van Noordwijk 1986, Janson & van Schaik 2002, Eadie 2015, although see also McGraw et al 2011, Chalk et al 2015 and O'Mara 2015 and Chapter 3 for contradictory evidence). Additionally, when feeding juveniles are likely to receive aggression from other group members (Pereira 1988a), being supplanted and displaced from such feeding sites. While matrilineal rank inheritance and agonistic support may buffer juveniles against aggression from older females (Periera 1989), adult males may pose a particular problem for juveniles. Adult and adolescent male baboons outrank all other group members (personal observation), and I found that adult males were aggressive to other group members at disproportionately high rates relative to their prevalence in the group, while also being more responsible for maintaining proximity.

Primates are distinctive in that groups are more often than not permanent associations between adult males and females, and their dependent offspring (van Schaik & Kappeler 1997, Kappeler & van Schaik 2002). Although chacma baboons are a highly dimorphic species (Popp 1983), they maintain cohesive groups and do not exhibit sexual segregation common to other dimorphic species (e.g. ungulates, Ruckstuhl 1998,

Michelena et al 2006). The constant presence of adult males may constitute a competitive threat to immatures' survival, not only through the potential for infanticide (e.g. Hrdy 1977), but also in terms of accessing resources. In this study I have demonstrated that although there were no significant age or sex related differences in the total time spent feeding; young juveniles obtained significantly more of their food from sources above the ground than either adolescent or adult individuals. Young juveniles' small size may therefore allow them to avoid direct competition with older individuals, who are unable to access the terminal branches due to their larger body size (e.g. Menard 1985, Menard & Vallet 1986). Additionally, young juveniles are likely to be more tolerated by older individuals (Pereira 1988a, Horrocks & Hunte 2002). Older juveniles however are less able to feed above the ground, while also less tolerated by adult males. However, by this age they may be more capable of foraging independently and efficiently, and so are able to tolerate increasing within-group competition.

Primate groups may be able to withstand the increased potential for within-group competition for resources by engaging in different activities at the same time, which may be particularly important considering the behavioural differences that exist between immature and mature individuals. The low levels of behavioural synchrony I reported may indicate that, due to the strong social bonds between group members (e.g. Silk 2007, Silk et al 2009) and their capacity for coordinating movements via vocalisations (Cheney et al 1996, Owren et al 1997, Meise et al 2011), primate groups are resilient against individuals attending to their own priorities. This may aid in reducing the costs of within-group competition as individuals can engage in other activities (e.g. resting in adult males, grooming in adult females, play in juveniles) while others feed, and then feed themselves while other individuals engage in other activities. Primates are likely to be at their most synchronised with others during feeding bouts (Clutton-Brock 1974, Kavanagh 1978), although they are also likely to be coordinated in their movements (King & Sueur 2011). However, I found that within-group competition, characterised by the amount of aggression received by an individual, leads to constrained travel routes. Individuals receiving aggression may return to previously visited food sources which are likely to be less optimal (Janson 1985, Johnson 1989).

Chacma baboon groups can remain cohesive even under conditions of low levels of behavioural synchrony and individual differences in travel routes.

A salient feature of hypotheses relating to the evolution of the juvenile period is the importance of encephalisation and increased brain size in primates relative to other mammals (Joffe 1997, Ross & Jones 1999, Ross 2004, Walker et al 2006, Barton & Cappelini 2011). This encephalisation is likely the result of the social complexity of primate groups (Barton & Dunbar 1997, Dunbar 1998, Dunbar & Shultz 2007). Given the wide inter and intraspecific variation in primate behaviour and group sizes (Chapman 2012), empirical studies that have set out to examine hypotheses relating to the evolution of the juvenile period provide conflicting support (e.g. Stone 2007, McGraw et al 2011, O'Mara 2015). Primates are highly flexible in their behaviour (Jones 2006, Dunbar & Shultz 2007, Amici et al 2008), and it is therefore likely that juvenile primates will behave in a manner commensurate with increasing their success under diverse conditions. For example, in an area of high predation risk, juveniles should behave in a manner consistent with minimising this risk (Janson & van Schaik 2002), but need not do so in areas of low predation risk. I propose that behavioural differences between juveniles and mature group members are indeed a consequence of juveniles' prioritization of activities and social partners that will both increase their chances of survival to adulthood, and also enhance their success as adults themselves (e.g. Periera 1988b) within the context of their social systems and social groups.

7.4. Recommendations for future research

Immature primates are notoriously difficult to study (Pereira & Fairbanks 2002, Barale et al 2015), and have been neglected by researchers as a consequence. Despite the difficulties that I encountered in my attempts to conduct focal observations on the youngest juveniles, I met with greater success with older juveniles. I have thus demonstrated that by studying juvenile primates alongside their older counterparts, it is possible to gain a better understanding of primate development. Future research should aim to ensure that juveniles are not studied in isolation, but rather in comparison

with older conspecifics. While primate behaviour varies greatly among species, and among different populations of the same species as a result of their unique ecological and demographic conditions, through studying individuals of all ages and sexes it may be possible to detect more generalised patterns. At a fundamental level, we still lack concerted efforts to examine the behaviour of juvenile primates, and considering that this juvenile period is arguably the single most important life history trait the distinguishes primates from other mammals (Pereira and Fairbanks 2002, Pereira and Leigh 2003), additional research is required.

Of particular interest for future research will be the use of the Kappa coefficient of agreement (Cohen 1960, Fleiss 1971, Siegel and Castellan 1988). Scan sampling is a standard in primatological research, and can be used to examine behavioural synchrony. Building up a database of studies, across multiple species and groups, will allow us to gain a better understanding not only of the juvenile period, but also the nature of primate societies in general**.** My findings that Kappa is robust against the number of behavioural categories used in its calculation indicate that such a comparative database may be possible even under different sampling regimes.

Additionally, while there is much knowledge about how groups of primates move through the landscape (e.g. Noser & Bryne 2007, Ren et al 2008, Willems & Hill 2009, Pebsworth et al 2012), we still know relatively little about how individuals within groups move (Bates & Byrne 2009). My study shows that between individual variation in movement, both in terms of the distance travelled and their tortuousity of movement, is not as simple as previously reported in animals (Wittemeyer et al 2007, Beisner & Isbell 2009). A better understanding of how individuals move as part of a group and their different constraints and pressures, both ecological and social, may enhance our knowledge of animals within groups. Importantly, the development of analytical techniques that can examine animal movements in three-dimensions (length, breadth and height) may help elucidate juvenile primates' use of vertical space, and the energetic requirements that this may impose.

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